

Ecological aspects on birds of prey ,
especially long-eared owl and
tawny owl

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ECOLOGICAL ASPECTS ON BIRDS OF PREY, ESPECIALLY

LONG-EARED OWL AND TAWNY OWL

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Abstract The importance of food for certain diurnal and nocturnal birds-of-prey was investigated with particular emphasis placed on the long-eared owl, and its relationship to the tawny owl. Prey choice, breeding biology and the population dynamics of the long-eared owl were examined in relation to changes in prey numbers and availability. During winter, the owl food consisted mainly of field voles, whereas during the breeding season other prey items such as water voles and birds became more important, due to the decreased number and lower availability of the field vole. The reproductive output recorded for local long-eared owl populations cannot explain the dynamic pattern observed in such populations, but presupposes a nomadic life strategy. Furthermore, the small rodent cycles within the long-eared owl's European range seem to be asynchronous. This is suggested to be an important reason for the evolution of nomadism in the species. The tawny owl was shown to be able to exploit open areas by hunting on the wing, thereby increasing its similarity to the long-eared owl in e.g. habitat utilization. Competition for food between these two species is inferred. The cause of this is the lower food overlap values recorded for neighbouring owls as compared to those for non-neighbouring owls. The reproductive output of long-eared owls decreased with decreasing distance from tawny owl neighbours. This is suggested to be a consequence of food competition. Two new hypotheses for birds-of-prey are proposed. Firstly, a hypothesis concerning reversed size dimorphism explaining both the direction and the degree of the dimorphism. This is based mainly on the idea that the availability of numerous prey items is important for the male during the early breeding season, and that the lowered relative cost of egg laying and the ability to transport relatively large prey items efficiently during the early nestling stage is important for the female. Secondly, that "resource depression", i.e. lowered availability of prey, is one reason for the regular nest spacing of birds-of-prey and that the degree of regularity of nest spacing depends on proportion of evasive prey in the diet of birds-of-prey. This is tested and supported by field data from 24 populations of birds-of-prey where birds and larger mammals in their diet are supposed to be evasive.			
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ECOLOGICAL ASPECTS ON BIRDS OF PREY, ESPECIALLY

LONG-EARED OWL AND TAWNY OWL

INGVAR N. NILSSON

Fil mag, Sm

Dissertation

1981



Birds of prey are a fascinating group among birds, a feeling I have in common with many biologists. Birds of prey have given me some of my most striking experiences in nature. For instance, listening to the territorial hootings of neighbouring tawny owls on a calm night in early spring, and watching a pair of hobbys hunting after swifts or swallows on a close summers' day.

Having this somewhat romantic approach to birds, I started to study the ecology of long-eared owls in 1973. My aim was to collect data on food choice and population dynamics, as part of an integrated predator - prey study, organized by my supervisor Sam Erlinge. However, after a few years I became aware of the fact that studying ecology was not just keeping up-to-date with literature on owl biology, but required a fundamental understanding of both general and theoretical aspects. In this my colleagues helped greatly. Accordingly, my interest in ecology changed from a naturalistic view to a more extended and theoretical approach. Thus, I became more interested in evolutionary ecology especially optimal foraging theory and competition.

Many people have, in one way or an other, contributed to the preparation of this thesis. Firstly, I want to express my thanks to my parents Margareta and Gustav Nilsson, Djäknebygd. They, so to say, laid the foundation stone of my interest in nature, giving me the opportunity of examining its whiles and its ways already in my childhood, and have, eversince, given me support in many ways. Most of my excursions at that time were made together with my brother Sven, and since then we have continued our field activities together.

From the time that I started my doctoral studies at the Department of Animal Ecology, both its Head, Per Brinck and my supervisor Sam Erlinge have supported and helped me in many ways. Sam also encouraged and gave me useful advice when I, for various reasons, could not obtain data as quickly as I would have liked. Furthermore, the warm and friendly atmosphere in the Ecology Building, and the discussions on various subjects, bot ecological and others, especially with members of the Wildlife Research Group at the department, helped me when things did not go my way.

Assistance in the field and/or in the laboratory was given by Catharina Cederlund, Sven-Olof Fransson, Mats Granath, Joyce Hansen, Carina Kullberg, Sven Lundberg, Dan Nordström, Ulf Sandnes, Jan-Olof Snygg, Anders Wetterin, and members of the Wildlife

Research Group. Information on small rodent numbers was given by Lennart Hansson, Inge Hoffmeyer, Boel Jeppsson and Fredrik Schlyter. Valuable comments and suggestions for most of the manuscripts were given by Sam Erlinge, Göran Högstedt, Hans Kristiansson, Olof Liberg, Jon Loman, Sven Nilsson and Torbjörn von Schantz. Görgen Göransson made the radio transmitters. Hilary Dow and John Veitch spent much time discussing and improving my English. My brother Sven Nilsson helped in many ways, and we have had many stimulating discussions on various aspects of ecology. Help with typing, preparation of the illustrations, and other practical things, especially when preparing this thesis, was given by Sune Arlebo, Steffi Douwes, Gunilla Lindquist, Inga Rudebeck, Birgitta Sundin and Ylva Zachrisson. I sincerely thank all these people and also others, the list of whom would have been too long to mention by name, for all their help and support during the study.

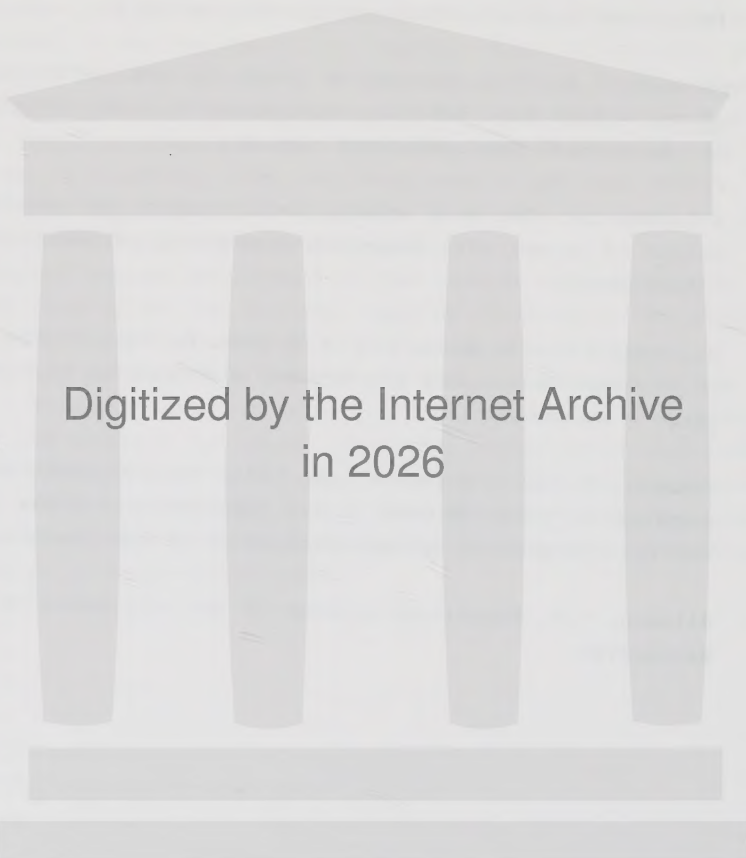
Financial support obtained from the Swedish Natural Science Research Council and the National Swedish Environment Protection Board (both via S. Erlinge) is also greatly acknowledged.

Last, and perhaps most importantly during the course of the years, I sincerely thank my wife Siv and our children - Torbjörn, Rickard and Henrik - for their continuing encouragement and their infinite patience with me and my, at times, irregular appearances at home and infrequent help in the household. They provided the necessary background for the fulfillment of this work. Accordingly, this thesis is dedicated to them.

LIST OF PAPERS

The thesis is based on the following papers, which will be referred to by their Roman numerals.

- I. Nilsson, I.N. 1981. Seasonal changes in food of the long-eared owl in southern Sweden. - *Ornis Scand.* 12 in press. (Reprinted by kind permission of the journal.)
- II. Nilsson, I.N. 1978. Hunting in flight by tawny owls *Strix aluco*. - *Ibis* 120: 528-531. (Reproduced by kind permission of the British Ornithologists' Union.)
- III. Nilsson, I.N. The prey weight, food overlap, and reproductive output of potentially competing long-eared and tawny owls. - Manuscript.
- IV. Nilsson, I.N., Nilsson, S.G. & Sylvén, M. Prey choice, resource depression, and the regular nest spacing of birds of prey. - Manuscript.
- V. Schantz, T. von & Nilsson, I.N. 1981. The reversed size dimorphism in birds of prey: a new hypothesis. - *Oikos* 36: 129-132. (Reprinted by kind permission of the journal.)
- VI. Nilsson, I.N. Population ecology of the long-eared owl - Manuscript.



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BACKGROUND AND SUMMARY OF RESULTS

On the following pages the reader will find some ecological notes on birds of prey, both diurnal and nocturnal, and how their life strategies are affected by their food resources. Food has long been considered as the most important factor in an animals life (e.g. Lack 1954), and so the ability to obtain food is one of the most important selective forces. Birds of prey are unique among birds in that they have evolved the ability of capturing mostly relatively large and agile prey. They all have sharp claws and hooked beaks, others have sharp eyes and still others a specialized hearing apparatus, all of which are adaptations which facilitate the detection, capture and subduing of prey (e.g. Norberg 1978, Newton 1979). These apparent adaptations indicate that the evolution of birds of prey, especially as they have different origins, has been possible only at the cost of relatively great morphological changes, and that dependence on vertebrate prey is a hard and arduous task.

Time and energy are limited resources in an animal's life and it has to make decisions continuously during its activities (e.g. Krebs 1978). During hunting, choices have to be made about e.g. where to go, what to catch, and when to select a new patch. All these decisions are important and have to be made as correctly as possible, enabling the animal to produce as many offspring as possible. The idea that foraging should be optimal has produced many studies, both theoretical and field studies (e.g. MacArthur & Pianka 1966, Pyke et al. 1977, Krebs 1978, Andersson 1981). The first result of foraging decisions is seen in the predator's diet. The food of long-eared owls was studied for three years (paper I). The aim was, predominantly, to record how seasonal changes in prey populations were reflected in the owls' diet. I found that the field vole was the predominant prey species during most of the year (August - April). For the rest of the year, the breeding season, the diet changed and consisted mainly of water voles and birds. These changes coincided with seasonal variations in the abundance and availability of prey populations, and the relatively rapid dietary changes indicated switching, which is predicted to be important by the optimal foraging theory. One point of contention was, however, the occurrence of relatively many prey species in the owls' diet during all seasons of the year, i.e. even when food specialization occurred. The long-eared owl was not the only predator in the study area. On the contrary,

the prey populations, in particular the field vole, were exploited by several predators; both birds and mammals with diurnal and nocturnal representatives (Erlinge et al. unpubl.). This means that any one of the predators could experience a great amount of diffuse competition (Pianka 1976); the food specialists more so than the generalist predators. The food overlap value is correlated with, and could be a measure of, the competition coefficient between two species. The more or less nomadic long-eared owl and the stationary tawny owl both occur in the Revlinge area, and both are nocturnal. The tawny owl has generally been believed to be restricted to perch hunting in woodland areas (e.g. Smeenk 1972). However, by using radio telemetry, I have shown that the tawny owl, in a mainly open area, can utilize the meadows rich in voles by hunting on the wing, and so increase its similarity to the long-eared owl in habitat utilization and prey choice (paper II). However, there are still differences (paper III). The food niche breadth value of the tawny owl was about three times that of the long-eared owl. When they had access to the same area, the tawny owl took more amphibians, water voles and birds, and less field voles than the long-eared owl. However, when considering the food overlap for neighbouring and non-neighbouring owls the values were lower for neighbouring owls, i.e. the opposite to that predicted considering the probability of similarity in prey species distributions. This suggests competition for food. As the species, then, could reduce each others hunting efficiency, a reduction in fitness, measured as reproductive output, could occur (Högestedt 1980). This effect would depend on the degree of overlap between the hunting areas of neighbouring owls, i.e. decrease with distance. The reproductive output of the long-eared owl did increase with distance from neighbouring tawny owl pairs. This is suggested to be an effect of reduced food competition when distances between their nests increase. For the tawny owl the opposite trend was observed. However, this is not, I believe, a result of any benefit for the tawny owl, but a result of local differences in food abundance. Thus, when a pair of tawny owls have a year rich in food, the probability that a pair of long-eared owls settle in that vicinity is greater, than when they have a bad year (paper III).

For a raptor pair nest spacing within its own population is usually more important for them than that of other species, according to the competition coefficients (paper IV). Competition between neighbouring raptor pairs with overlapping hunting areas

is experienced by them as a decrease in the number of prey individuals seen. Usually, this decrease has been thought of solely as an effect of exploitation. However, prey individuals have, to a variable extent, the ability to detect and react evasively to an approaching predator and so be less available for some time onwards (Goss-Custard 1970, Charnov et al. 1976). Thus, after the appearance of a predator in an area the availability of some prey species is reduced for a period of time, and the predator arriving next will experience "resource depression" during that time (Charnov et al. 1976). With these considerations and the suggestion that birds and larger mammals are the most evasive prey groups, the hypothesis was suggested that an increasing proportion of such prey in the predators' diet should be reflected by an increasing degree of regularity of nest spacing in raptors. The hypothesis was preliminary tested (paper IV). A significant positive correlation was found between the proportion of birds and larger mammals in the predators' diet and the degree of regularity of nest spacing, supporting the hypothesis. It is difficult, though, to differentiate between the effects of exploitation and resource depression, both of which would be expected to produce regular nest spacing, if the nests were centrally situated in the hunting areas (Orians & Pearson 1978). However, it is difficult to explain the varying degree of nest spacing, observed in raptors, solely as an effect of exploitation.

Even the relationship between a pair of raptors is unique for the majority of birds. Usually, the male provides the female and the nestlings with all their food during the incubation and the early nestling period, supplemented by the female after that period. Furthermore, they exhibit a varying degree of size dimorphism; from about equal weight to a condition where the female is about twice as heavy as the male (Newton 1979). This reversed size dimorphism in birds of prey, i.e. females being larger than males, has received a lot of attention and given rise to many suggestions as to its causes (paper V; for a review see also Newton 1979, Andersson & Norberg 1981). For birds of prey the slope of the egg size - body weight relationship is less than that of the BMR - body weight relationship (Ricklefs 1974). Thus, by increasing the size of the female the relative cost of egg-laying is reduced. This is suggested to be one reason for the female being larger than the male (paper V). In addition, when the food demands of the young increase, a larger female can transport larger prey and

select from a wider spectrum of prey species. The male benefits from being small, thereby reducing the energy expenditure it uses for hunting and having access to a greater number of prey. Furthermore, the greater the weight of the prey the greater the importance of reducing proportionate wing load, and the smaller the relative size of the prey the greater the number of provisioning trips and, consequently, the greater the cost of being large for the female.

The distribution, breeding success, and population dynamics for long-eared owls was recorded in the Revinge area (paper VI). The number of produced broods in the study area of about 45 km² varied tenfold, mainly in accordance with small changes in field vole numbers. The average density was about 0.2 pairs/km². About 80 % of the nests produced fledged young. The average clutch size was about 4.6 eggs, and the successful nests fledged about 2.9 young. The nestling mortality (35 %) occurred mostly during the first week after hatching, probably due to starvation. After leaving the nest, and when still dependent on the adults, about 20 % of the young disappeared. Considering these results together with data on mortality rates obtained from recoveries of ringed birds, a low capacity for increase in the local population is obtained. This cannot explain the dynamic patterns observed in local populations where the small rodents are cyclic, and thus underline the nomadic life strategy of the species (see Andersson 1980). This nomadism seems to have evolved together with the asynchronous small rodent cycles. However, a tendency for site tenacity seems to occur, at least in areas where the change in numbers of the prey species is relatively small, and it is suggested that nomadism is more pronounced in juveniles than in adults.

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SEASONAL CHANGES IN FOOD OF THE LONG-EARED OWL IN
SOUTHERN SWEDEN

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ABSTRACT

The food of a long-eared owl population was examined in relation to the abundance of important prey during three years in an open field area in southern Sweden. About 7800 individual vertebrate prey items were identified.

The prey biomass consisted mainly of field vole (80 - 90 % during winter), water vole (15 - 65 % during summer), birds (10 - 60 % during summer), and wood mouse (5 - 25 % during the year).

The prey choice showed pronounced seasonal and smaller yearly changes. During winter one prey species (field vole) constituted most of the food: in summer the diet became more varied, probably due to decreased availability of field voles and increased availability of some larger prey (water voles and birds). In summer two to four prey species made up the bulk of the food. The food niche was about three times broader in summer than in winter.

The total number of prey categories included in the diet was higher in winter and thus showed an opposite seasonal pattern as compared with the number of prey species forming the main food.

Calculated preference indices were high for the field vole in autumn and winter, and for the wood mouse in summer, which may be explained by changed profitability to the owl of the habitats.

Predictions from optimal foraging theory are discussed in relation to the field data.

INTRODUCTION

About 300 000 individual prey items have been identified from pellets of the long-eared owl (Asio otus L.) in Europe (e.g. Tinbergen 1933, Uttendörfer 1952, Hamar and Schnapp 1971, Schmidt 1973 - 74). However, most of these pellets were collected during winter when the owls gather in flocks, and few samples covered more than one season. Consequently, these samples give a biased picture of the relative importance of different prey species for the long-eared owl during the year.

Previous studies of the food choice of the long-eared owl in Sweden only briefly examined the choice of prey in relation to prey densities.

The aim of this study was to relate the food intake of the long-eared owl to changes in the availability of the main prey populations throughout the year.

STUDY AREA

This study was undertaken in the Revinge area, 20 km east of Lund, in southern Sweden. The study area, of about 4300 ha, was used for farming until 1964 but since then it has been a military training zone. About half the area comprises open fields grazed by cattle, while other parts consist of sandy hills and wet meadows and marshes on peat soils. Small pine plantations and deciduous woods are scattered throughout the area and a large

beech wood and Lake Krankesjön are situated in the middle.

MATERIALS AND METHODS

Pellet sampling and analysis

Pellets were collected once or twice every month, at roosts or breeding sites of the long-eared owl through the years 1974 - 1976 except for February, September and December, 1976, when no samples were collected.

In the pellet analysis all skulls and jaws from mice and voles were removed and counted separately for every sample, to estimate the minimum number of individuals. The two Apodemus species occurring in the area could not always be separated and were combined. The smaller A. sylvaticus occurs in both woods and open fields, but the larger A. flavicollis is almost completely restricted to woodland (Hoffmeyer and Hansson 1974). Very few individuals were identified as adult A. flavicollis (large skulls and jaws), so almost all Apodemus individuals were probably A. sylvaticus. Pellets were also examined for both humerus and femur of the water vole which were then paired according to size to estimate the number of individuals. This estimate was chosen if it exceeded the number based on skull parts, as it usually did. All bones and cranial parts from lagomorphs and birds were used for estimation of prey numbers; humeri were particularly useful for estimating both the number and weights of eaten birds. The weights used to determine the energetic importance of different prey species, apart from birds, are given in Table 1. Each pellet sample, i.e. pellets collected at one place, was treated as a unit and analysed separately. The samples were always collected thoroughly at the same sites, so the time intervals during which they were produced were known. The food choice was evaluated on a monthly basis. When a pellet sample was produced over a period of two calendar months the number of prey individuals were divided accordingly. Then all prey categories in the samples were summarized for each month to give the food choice in the area for each month (Appendix 1). To estimate the food composition by biomass, the number of individuals were multiplied by the weights in Table 1 and weights for birds (divided in six weight classes). During the winter, when the owls gather in day roosts, large samples were sometimes collected (estimated at more than 1500 prey individuals). From these a subsample containing about 20 % of the pellets was

TABLE 1

Weights (g) used to estimate the relative importance of long-eared owls' prey during the year. Birds are excluded.

Prey species	March - May	June - Sept.	Oct. Febr.	The whole year
Mole <u>Talpa europea</u> L.				100
Common shrew <u>Sorex araneus</u> L.	10	10	7	
Pygmy shrew <u>S. minutus</u> L.				3
Water shrew <u>Neomys fodiens</u> Pennant				10
Bats <u>Chiroptera</u>				15
<u>Lagomorpha</u>				200
Bank vole <u>Clethrionomys glareolus</u> Schreber	21	20	16	
Field vole <u>Microtus agrestis</u> L.	30	30	21	
Water vole <u>Arvicola terrestris</u> L.	115	115	100	
Wood mouse <u>Apodemus sylvaticus</u> L.	21	21	18	
House mouse <u>Mus musculus</u> L.				15
Common rat <u>Rattus norvegicus</u> Berkenhout				100
Weasel <u>Mustela nivalis</u> L.				80

randomly taken and analysed.

The reliability of pellet analysis has been discussed in several papers (e.g. Southern 1954, 1968). Raczyński and Ruprecht (1974) found that 21 % of the prey individuals consumed by long-eared owls was not present in the pellets. Similar losses were also found for the tawny owl Strix aluco L. (16 %) and to a lesser extent for the barn owl Tyto alba Scopoli (8 %) (Raczyński and Ruprecht 1974). Furthermore they found that the rate of loss of bones was higher for young prey and in pellets from young owls. Also, Goszczyński (1976) noted a loss in numbers for adult barn owls (0 - 6 %). The loss of cranial parts varies for different prey species, and, for instance, is higher for wood mouse and bank vole than for field vole (own observations). This was also reported by Southern (1968), who found the losses in the number of small mammals in pellets from the tawny owl to be 15 - 60 %. However, this method should be acceptable for examining seasonal and yearly variations in the diet of one owl species in one region.

Prey populations

The densities of small mammals in the Revinge area 1974 - 1976 were estimated by Dr. Lennart Hansson, Uppsala (unpubl.), by using the Standard Minimum Method (Grodzinski et al. 1966, Hansson 1969). The densities of the three most common small mammals for different habitats are shown in Appendix 2. The general population pattern for small mammals in the area was a yearly maximum in September - October and a minimum in May - June (Hansson 1968, 1971). The increase during summer and autumn was rapid, but the decrease during winter and spring was slow and seemed to be almost linear (Hansson 1968, 1971, unpubl.). This pattern was the same as that found in the adjoining woodland (Hoffmeyer and Hansson 1974). The water vole density in the Revinge area was only measured during the autumn 1975. The distribution was clumped, and consequently the mean density was difficult to determine. However, the density was estimated as 5 - 10 animals per ha in wet meadows on peat soils and less than 5 animals per ha in fields on mineral soil (Jeppson and Schlyter unpubl.). The yellow-necked mouse population, almost exclusively wood-dwelling (Hoffmeyer 1973), reached high densities in the autumns of 1975 and 1976 (particularly in the latter year) in a central beech wood following a good beech mast in both these years (Hoffmeyer pers. comm., own observations). Bird densities were not systematically measured during the study. However, there are only small annual variations. The density increases during the autumn when migrating birds (e.g. small passerines) pass through the area, and in late spring and summer when young birds leave their nests. It was of particular relevance than all young starlings Sturnus vulgaris L. left their nests almost simultaneously about the first week of June every year in this area.

RESULTS

Seasonal changes in the food

The overall food biomass of the long-eared owl during 1974 - 1976 consisted of 90 % small rodents (Fig. 1). The field vole was the most important prey item and it constituted two thirds of the estimated prey biomass. Secondary in importance were water vole, wood mouse and birds (mainly thrushes and starlings).

Two main periods of the year show considerable differences; the breeding season (April - August), and the over-winter period (September - March; Fig. 2, Appendix 1). The latter period was charact-

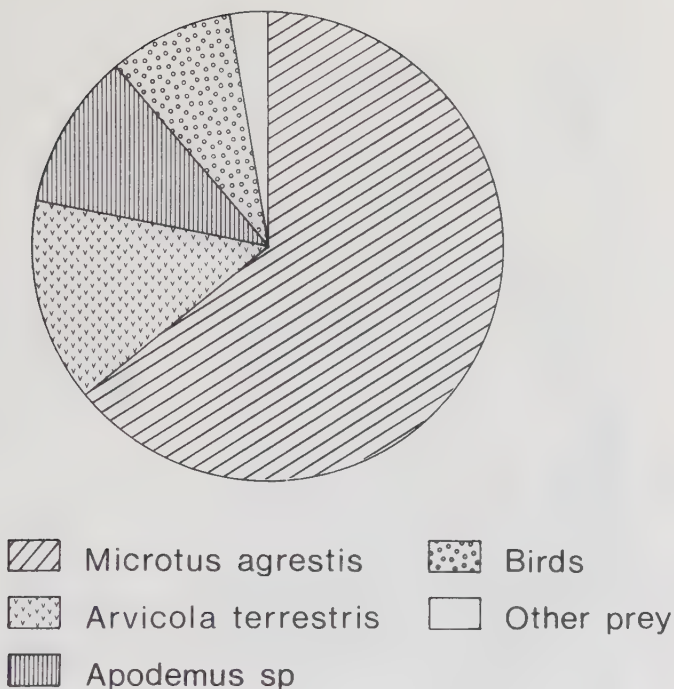


Fig. 1. Food spectrum (% of biomass) of the long-eared owl during 1974-76 (7811 prey individuals).

erized by heavy predation on the field vole, viz 70 - 90 % of the prey individuals or 67 - 94 % of the prey biomass. The rest of the food consisted mainly of Apodemus, but water vole, insectivores, bank vole and small passerines also occurred.

During the breeding season the diet became markedly less specialized on field voles. In April and May there was a decrease in the proportion of field voles and an increase in water vole, wood mouse and/or birds. The broadest food spectrum occurred in June and July (Fig 3). At that time four prey categories, field vole, water vole, Apodemus spp., and birds comprised at least 95 % of the prey biomass. Their relative importance showed great annual variation (Table 2).

Insects, exclusively beetles, were usually found singly, throughout the year (Appendix 1). The species most often

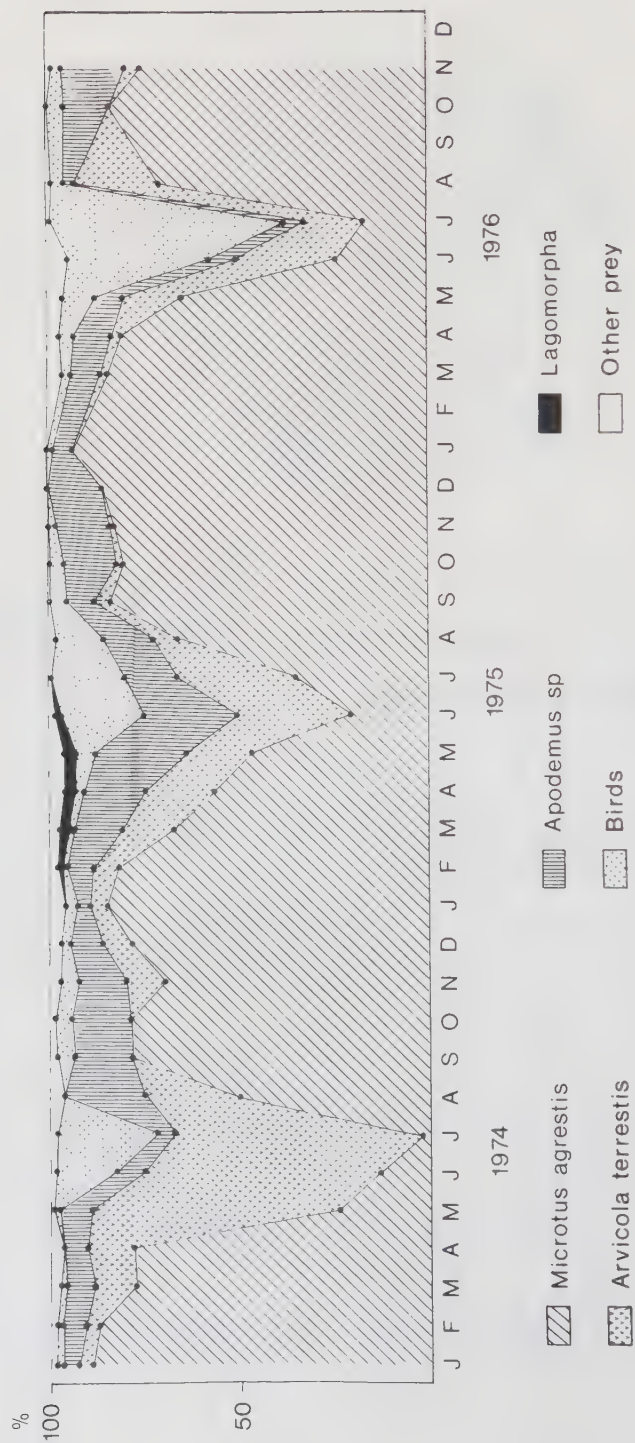


Fig. 2. Seasonal changes in the food biomass (wet weight) of the long-eared owl during 1974-76.

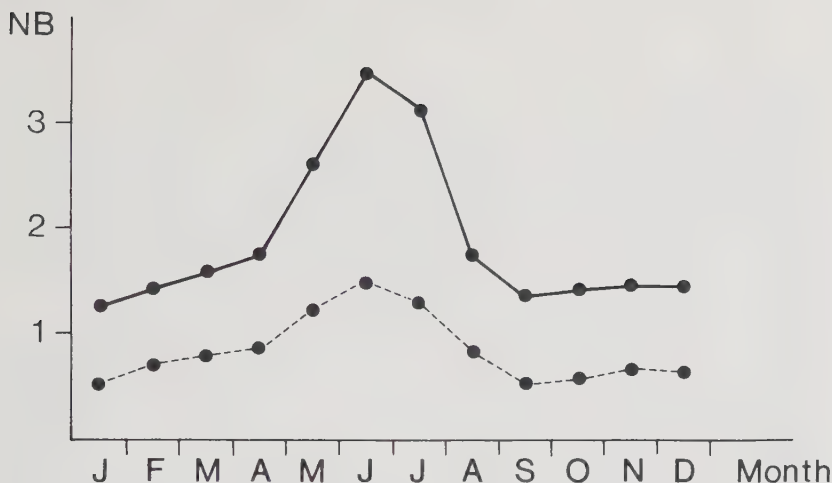


Fig. 3. Seasonal changes in food niche breadth (NB) in the long-eared owl (mean values for 1974-76) using the indices $NB = (\sum p_i^2)^{-1}$ (Levins 1968; solid line) and $NB = -\sum p_i \cdot \ln p_i$ (dashed line), where p_i is the proportion of species i in the diet. The niche breadth values were calculated on data given in Appendix 1.

encountered was Dytiscus marginalis, but Geotrupes, Melolontha and Carabus species also occurred.

Food preference and niche breadth

Preference index values were calculated for some small mammal species pairs for periods when population data were available. The index used (Table 3) was originally proposed by Jacobs (1974, cited in Cock 1978), and is useful when exploitation of prey is negligible. It shows that wood mice were preferred to field voles during summer. The reverse was the case during autumn and slightly during spring. Overall, shrews do not appear to be selected. The strong preference for field vole over water vole, during spring and autumn was not detected during the summer.

The average food niche breadth was calculated for the different months (Fig. 3). There was a marked increase in the food niche breadth from May to July due to the decreased importance of field vole in the diet.

TABLE 2

Monthly differences in the food of the long-eared owl between the years 1974 - 76. Based on the number of prey individuals corresponding to the percentages in Appendix 1 (the smallest prey categories were combined to obtain sums greater than ten).

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<u>1974/75</u>												
χ^2	16.8	12.5	24.0	33.9	37.7	32.5	19.3	4.8	3.4	0.74	13.8	13.0
df	4	4	5	4	4	4	3	2	2	2	2	3
p	0.002	0.014	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.09	0.19	0.69	< 0.001	0.005
<u>1975/76</u>												
χ^2	19.8		49.1	51.7	32.0	27.3	10.4	3.8		0.03	1.87	
df	2		5	5	5	4	3	2		1	1	
p	< 0.001		< 0.001	< 0.001	< 0.001	< 0.001	< 0.015	0.15		0.85	0.17	
<u>1974/76</u>												
χ^2	10.1		12.3	24.1	49.3	14.9	9.1	9.4		0.23	6.7	
df	3		5	5	4	4	2	2		1	2	
p	0.017		0.03	< 0.001	< 0.001	0.005	0.011	0.009		0.63	0.035	

TABLE 3

Preference index values (mean for 1974-76) for some small mammal pairs in the food of the long-eared owl.

Preference index = $(N_{1,e} / N_{2,e} - N_1 / N_2) / (N_{1,e} / N_{2,e} + N_1 / N_2)$, where $N_{i,e}$ is the numbers eaten of species i , and N_i is the population density of species i (Cock 1978, index 8). The index goes from minus one to zero for negative preference, and from zero to plus one for positive preference. Data on the small mammal populations were obtained from Hansson (Appendix 2 and unpublished; mean values for abandoned fields on peat soil and mineral soil were used) and from Jeppsson (unpublished).

	Mar/Apr	May	Jun	Aug	Sep
Field vole					
Apodemus	0.2	-0.2	-0.4	-0.7	0.7
Field vole					
Sorex	-	-	0.4	0.6	1.0
Apodemus					
Sorex	-	-	0.6	0.9	0.9
Field vole					
Water vole	1	0.2	-0.1	-	1

DISCUSSION

Food

Small mammals, especially Microtus species, are the most important food of the long-eared owl as noted in several other studies (e.g. Schmidt 1973-74, Marti 1976, Källander 1977a, and further references in these papers). The importance of other prey categories may have been underestimated in these studies as they mostly did not consider seasonal changes. A similar pattern of spring decrease in the proportion of voles taken and a corresponding increase in the importance of mice (Peromyscus) has been recorded in North America (Marti 1974, Voight & Glenn-Lewin 1978).

Although widely distributed in northern Europe, the water vole is generally reported to be of little significance as food for long-eared owls. However, Hagen (1965) found a relatively

high frequency of water voles in Norway (7.6 % of the vertebrate prey individuals) as did Bohnsack (1973) in Germany (up to 9 % of the prey individuals). In a ural owl Strix uralensis population in central Sweden, Lundberg (1976) found that about 37 % of the prey individuals given to the young were water voles. In the present study up to 40 % of the prey individuals during parts of the summer were water voles. The tawny owls in the study area have up to 15 % water voles in their diet (Nilsson unpubl.).

In urban areas a high proportion of birds occur in the food of long-eared owls; up to 80 % in Dutch cities (Tinbergen 1933), and 30 % in the city of Malmö, Sweden (Hillarp 1971). Usually , however, the percentage of birds in the diet is low. In this study birds constituted up to 34 % of the prey individuals during summer.

Herrera and Hiraldo (1976) examined the food niches of European owls and concluded that the food niche of the long-eared owl as indicated by Shannon's index, were broader in Scandinavia than in Middle Europe (Table 4). The value they presented for Scandinavia, however, is not applicable to all parts as they only used Hagen's (1965) data from Norway. There does not appear to be any latitudinal trend in the food specialization of the long-eared owl (Table 4; see also Källander 1977a and Järvinen 1977).

Optimal foraging

Optimal foraging theory (e.g. Schoener 1971, Ellis et al. 1976, Pyke et al. 1977) predicts that a predator should widen its food niche when the preferred food types become scarce, and shrink it when they become abundant. This was observed in the long-eared owl during spring and autumn, respectively (Fig. 3). During May and June, when food abundance increased, the expected decrease in food niche width was not observed. However, the use of the niche breadth index may be inappropriate during this period, since the environment was markedly changing; also despite the increased food abundance during this period, the denser vegetation cover could have resulted in a similar or decreased encounter rate with the rodents. This would mean that food accessibility for the long-eared owl would not increase in the peat soil areas. If so, the number of prey species included in the diet should remain the same, as was observed, (Fig. 4). The expanded food niche breadth during May and June could also have been caused by the increased energetic demands at breeding (Schoener 1971).

TABLE 4

Food niche breadth for the long-eared owl in Europe, measured with Shannon's index $H' = -\sum p_i \cdot \ln p_i$ (modified from Källander 1977a).

Area	H'-value	Data source
Sweden (summer)	0.94 - 1.00	Gerell (1968), Lundin (1960), Källander (1977a)
Sweden (winter)	0.69 - 1.18	Gerell (1968), Lundin (1960), Källander (1977a)
Sweden	0.91 - 1.11	This study (values for the whole year)
Finland	0.47 - 0.86	Soikkeli (1964), Sulkava (1965)
Scandinavia	1.47	Hagen (1965) in Herrera and Hiraldo (1976)
Middle Europe	1.01	Uttendörfer (1939) in Herrera and Hiraldo (1976)

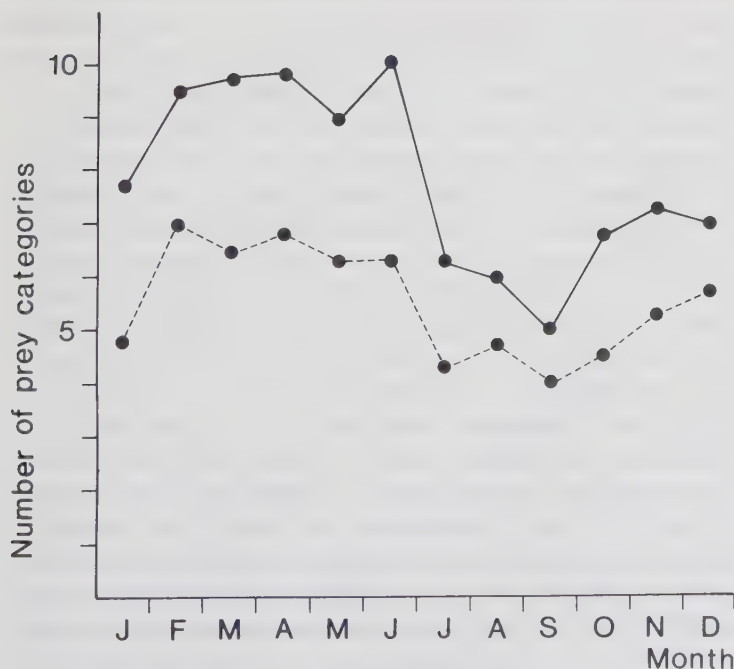


Fig. 4. Total number of vertebrate prey categories (solid line) in the food of the long-eared owl (mean values for 1974-76). Birds were separated into six weight classes. The number of mammal species in the diet is shown by the dashed line.

In summer, with a continuously increasing rodent population but with a relatively constant vegetation cover, the number of species in the diet should decrease (e.g. Pyke et al. 1977). This was observed (Fig. 3 and 4). However, the relative importance of the dominant species included in the diet was different in the three years (Fig. 2). This supports the idea that both total food abundance and relative food abundance could be important when evaluating optimal diets in the field (Estabrook and Dunham 1976, Stenseth and Hansson 1979).

The fact that the long-eared owl always included many prey species in its diet (Fig. 4) could indicate that (1) the total prey availability was limited due to strong diffuse competition, (2) the owls sampled many habitats throughout the year in preparation for changes in the populations of different prey (Pulliam 1974), (3) the owls hunted opportunistically in selected patches (Royama 1970), or (4) the nutritional needs dictated a varied diet. Considering the fitness sets of prey pairs, the following conclusions can be drawn. When the prey availability is low and the fitness set curve is concave, i.e. the two prey types must be hunted in different ways, then the predator should be selective. Conversely, when the fitness set curve is convex, i.e. the prey types can be hunted in similar ways, the predators should take them in the proportion they are encountered (Lawlor and Maynard Smith 1976, Stenseth unpubl.). I think that case (1) applied because of the high predation pressure (Wildlife Research Group, unpubl.). This could then result in a need for the owls to hunt in many different habitats, and, if the prey types have convex fitness sets, perhaps hunt opportunistically in the habitats (similar to (2) and (3)).

A clear functional response of the long-eared owl to the changes in field vole population density was not detected in this study. There was in fact a weak inverse relationship between proportion of voles in the diet and density of voles in the peat soil areas from May to July. This was probably caused by the decreased availability of voles due to thick ground vegetation and the fact that alternative prey were available in other habitats. During the rest of the year the proportion of voles in the food was high irrespective of their abundance. One interpretation could be that a predator in a multi-prey situation has the option of switching to alternative prey (Murdoch 1969). This switching seems to occur at a certain threshold level for the preferred

prey (Goss-Custard 1977). This level is dependent on the relative profitability of alternative prey at that time.

Food preference and availability

In a changing prey environment with patchily distributed food a predator is forced to continuously sample the profitability of different prey species within the patches in order to be efficient. Since the availability in different habitats changes, much switching should occur (Cornell 1976). This seems to be the case in this study. However, when calculating food preferences through the year (Table 3). I did not take into account the possibility of the various prey populations showing differential changing availability: only density estimates were used. During May-June the vegetation in the peat soil areas grows very fast and completely covers the ground by late May (Balsberg pers. comm., own observ.). This greatly decreases the availability of the field vole which has its highest densities in this habitat. The wood mouse is absent from peat soils during spring (Hansson 1968, Hoffmeyer and Hansson 1974). During the same period the vegetation cover of the drier soils, inhabited by wood mouse and a few field voles, does not change as much and thus the availability here is less affected. This means that the profitability of drier soils may rise, in relation to that of peat soils and during this period the owls probably hunt to an increasing extent in the former habitats. This could, at least partly, explain the observed preference for wood mouse during this period. During the autumn the vegetation cover decreases and the availability of the field vole increases, resulting in a shift back to proportionally more field voles (Table 3). Availability probably also affects the change from a high preference for the field voles over water voles during the winter, to no difference in preference during summer. Two factors may increase water vole availability during the summer. Firstly water voles mostly live underground on dry soils during the winter and then shifts to peat soil and marshes during the spring (Jeppsson pers. comm.). Secondly activity "above-ground" is higher during spring and summer (Gaisler and Zejda 1973). However, as mentioned earlier, the increasing density of the vegetation cover during spring in the wet habitats nullifies this increase. Availability of both water voles and field voles is similarly affected during the summer. Further reasons for the "non-preference period" could be that the recog-

nition time is too long to establish a preference for either vole (Hughes 1979), that they have similar net energy values, or a convex fitness set curve (see above). Therefore, when hunting in wet habitats, the owls take vole prey in the proportion they are encountered.

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APPENDIX 1

The food of the long-eared owl in the Revinge area during 1974, 1975 and 1976. The figures are the percentage of the total number of prey individuals (excluding beetles) during each month. Occurrence of beetles is indicated by crosses.

Month	Mole	Common Shrew	Pygmy Shrew	Water Shrew	Bank Vole	Field Vole	Water Vole	Wood Mouse	House Mouse	Lago-morpha	Weasel	Birds	Amphi-bia	Beet-les	Number of prey indi-viduals
1974 Jan		0.6	1.9		1.9	88.7	0.8	5.6				0.5	x		519
Feb		1.2	2.1		2.1	85.9	0.8	7.5				0.4	x		603
Mar		2.6	0.5		1.3	82.3	2.5	9.8		0.2		0.8	x		510
Apr		1.7	0.8		4.6	82.7	3.0	7.2					x		237
May		6.5	0.7			44.6	28.0	18.0				2.2	x		139
Jun		2.7	0.9			34.7	31.3	17.9	0.9			10.7	0.9	x	112
Jul		5.9	14.3			7.1	42.9	14.3				21.4		x	14
Aug						60.7	5.9	27.5						x	51
Sep		1.2	0.2		0.5	80.7		16.0	0.2			1.2	x		207
Oct		1.2	0.2		0.5	80.7		16.0	0.2			1.2	x		207
Nov	0.3	1.0	0.7		1.7	78.8	2.1	14.4				1.0	x		145
Dec	0.2	3.5	1.0		1.6	80.4	1.7	10.3				1.3	x		239
1975 Jan		7.4	1.4		1.4	83.0	1.1	3.9				1.8	x		189
Feb		5.8	1.2	0.2	1.1	81.2	1.5	8.6		0.1		0.3	x		622
Mar		7.2	1.8		1.2	69.9	3.3	15.2		0.4	0.1	0.9	x		402
Apr		7.6	1.8		1.7	61.1	4.5	21.0		0.5	0.2	1.6	x		231
May		3.5	1.0		4.1	51.6	4.4	32.1		0.6		2.7	x		157
Jun		2.3	0.5		0.5	35.5	10.5	42.3		0.2		8.4	x		220
Jul		2.1				57.9	10.5	22.1				7.4			63
Aug		3.0			0.6	75.0	1.5	14.6			1.3	4.0			158
Sep		0.9				89.8	0.9	7.5				0.9			71
Oct		0.3	0.2		0.2	83.1	0.3	14.7				1.2			355
Nov		0.1	0.1		0.1	84.2	0.1	14.8				0.6			350
Dec						83.7		16.3							118
1976 Jan					0.5	92.9		6.1				0.5			212
Feb															-
Mar		1.4	1.0		0.7	85.4	0.4	9.5				1.2	x		591
Apr		1.5	0.4		0.6	81.6	0.6	11.9		0.4		2.4	x		465
May		5.8	1.6		1.6	70.4	4.0	9.3		0.3		4.5	x		189
Jun		9.3	1.9			46.9	10.5	13.6		0.6		16.7			81
Jul		1.9	1.9			41.5	7.5	13.2				34.0			27
Aug		2.8				86.1	5.6	2.8				2.8	x		36
Sep															-
Oct						84.3		12.5				3.1			32
Nov		0.4			1.9	78.4	0.8	17.8				0.8	x		259
Dec															-
Average		2.8	1.1		0.9	71.1	5.5	14.1		0.1		4.4			7811

APPENDIX 2

Mean densities (animals/ha) of small mammals in open habitats in the Revinge area 1974-1976. Data from Hansson (unpubl.) according to trapping with the Standard Minimum method (extrapolation estimates; Grodzinski et al. 1966). The trapping periods were: first half of June = I, end of July to beginning of August = II, and middle of September = III.

	1974			1975			1976		
	I	II	III	I	II	III	I	II	III
Field vole (<i>Microtus agrestis</i>)									
Abandoned fields on peat soil (about 400 ha)	5	54	54	22	54	54	5	54	54
Abandoned fields on mineral soil (about 400 ha)	1	20	20	1	20	20	1	20	20
Grazed fields (about 2900 ha)	2	0	0	2	0	0	2	0	0
Wood mouse (<i>Apodemus sylvaticus</i>)									
Abandoned fields on peat soil	0	0	5	0	0	5	0	0	5
Abandoned fields on mineral soil	2	2	14	2	2	14	2	2	14
Grazed fields	1	1	1	1	1	1	1	1	1
Common shrew (<i>Sorex araneus</i>)									
Abandoned fields on peat soil	4	33	33	4	7	7	4	7	7
Abandoned fields on mineral soil	0	1	1	0	1	1	0	1	1
Grazed fields	0	0	0	0	0	0	0	0	0

HUNTING IN FLIGHT BY TAWNY OWLS *STRIX ALUCO*

Predators can detect prey in two different ways, by active search or by sitting and waiting. Most authors state that the Tawny Owl *Strix aluco* belongs to the latter group, and does not hunt on the wing but waits on a perch from which it detects and dives upon the prey (e.g., Southern 1954, Southern & Lowe 1968, Smeenk 1972). Smeenk drew the conclusion that the Tawny Owl is confined to woodland and the edges of wooded areas in its hunting. However, Rosenberg (1961) has said that the Tawny Owl sometimes hunts when flying low over open areas.

The aim of my study was to examine the hunting techniques of Tawny Owls in territories containing small woods and open ground. The work was carried out in the Revinge area of Skåne, southern Sweden. The area consists of sandy hills, abandoned fields (mostly used as pasture), marshes and wet meadows sometimes vegetated with bushes. Small stands of deciduous trees and pine plantations are scattered over the area which has been used for military training purposes and cattle-grazing since about 10 years ago.

During the periods 23 February–6 March and 26 April–8 May 1975, two Tawny Owls were radio-tracked in their territories. From their weights (546 and 593 g, respectively) and their calls the owls were judged both to be females. The first owl had not started to breed, and the second had abandoned fresh eggs. The two owls were tracked by night, when out of their day-time roosts, for 54 and 33 hours, respectively.

The transmitters (27 MHz) were modified from the type described by Nicholls & Warner (1972). A loop-antenna was put around the body of the owl and a second loop loosely around the neck. The relative weights of the transmitters were 5.1 and 4.2% of the owls' body weights, and their lifetimes were 11 and 14 days, respectively. The transmitters emitted a pulsed signal (about 80 pulses/min). The receiver had also a loop-antenna. By this arrangement, firstly, the bearing (direction) to the transmitter could be established with good accuracy. Secondly, a rough estimate of distance, according to the volume of the signal, could be obtained. Thirdly, when the owl turned its body, sitting on a perch or in flight, this was heard at the receiver as a change in the intensity of the signal. On occasions, direct visual observation was possible and confirmed these interpretations of the radio signals. Radio-tracking was performed as continuous cross-triangulation, at a distance of 50–100 m (occasionally more, or less), as I walked around to keep in contact with the bird, and to ascertain its position or hunting area. At this range the accuracy of the bearings are within a few metres. The owls did not appear to react to me, or the transmitters, and sometimes were seen passing by at a distance of only 5 m. During the triangulation, time, position or hunting area, habitat, and type of activity were recorded.

RESULTS

The owls devoted about one third of their active time (see above) to hunting on the wing (Table 1). When visible (in moonlight) they were seen to be flying 2-3 m above ground in marsh or grassland between the small clumps of bushes. This flight was slow, frequently interrupted with glides, and only used in open habitat. When the owl was hunting on the wing it flew to and fro over an area of about 30×50 m, quartering the area in a zigzag pattern. This could be monitored with the receiver alone, but was sometimes also seen simultaneously. When one area had been searched, if the behaviour was continued, the owl flew some distance (usually 100-200 m) before resuming the zigzag searching pattern, and so on. During a period of several days, almost the whole home-range was hunted over. Details of habitat utilization have been given by Nilsson (1977).

TABLE 1

Distribution of activities (per cent) in two radio-tracked Tawny Owls. See text for further explanation of activity categories

Activity	Sitting (probably resting)	Sitting, frequently interrupted by short flights (probably hunting from a perch)	Hunting in flight	Total time (min)
Owl No. 1 (24 Feb.-6 Mar., 1975)				
24-25 Feb.	8.9	27.0	64.1	315
25-26 Feb.	18.4	30.6	51.0	245
26-27 Feb.	46.5	41.2	12.4	340
27-28 Feb.	34.3	34.3	31.3	670
28-29 Feb.	35.4	4.6	60.0	325
3-4 Mar.	22.7	33.3	43.9	330
4-5 Mar.	31.3	40.6	28.1	320
5-6 Mar.	17.4	70.6	12.0	718
Overall	26.9	39.6	33.6	3263
Owl No. 2 (26 Apr.-8 May, 1975)				
Overall	49.0	9.0	42.0	1977

Usually, hunting on the wing alternated with hunting from a perch and/or resting; the last two activities could not be separated with certainty, although the character of the pulses (constant or changing in volume) served as an indication. Periods when the owls were sitting almost immobile (indicated by pulses of constant volume), usually in the woods, have been classified as resting (Table 1, column 1), and periods when the owls were sitting but turning now and then (indicated by pulses of changing volume) have been classified as hunting from a perch (Table 1, column 2). In the latter cases the owls also made frequent short flights (at least one every five minutes) returning to the same perch or another one.

During the hours of darkness, when the owls were active, the different activity types succeeded each other in an irregular way giving a pattern exemplified in Figure 1.

No certain captures of prey were seen during the radio-tracking. However, several times during the tracking there were indications at least of attempts to capture prey, both in flight and from a perch. On these occasions the pulse volume suddenly went low and the signal sometimes even disappeared for up to five minutes. The owl was then presumably on the ground behind a tussock, or other natural radio-opaque object, but this was not actually confirmed by sight.

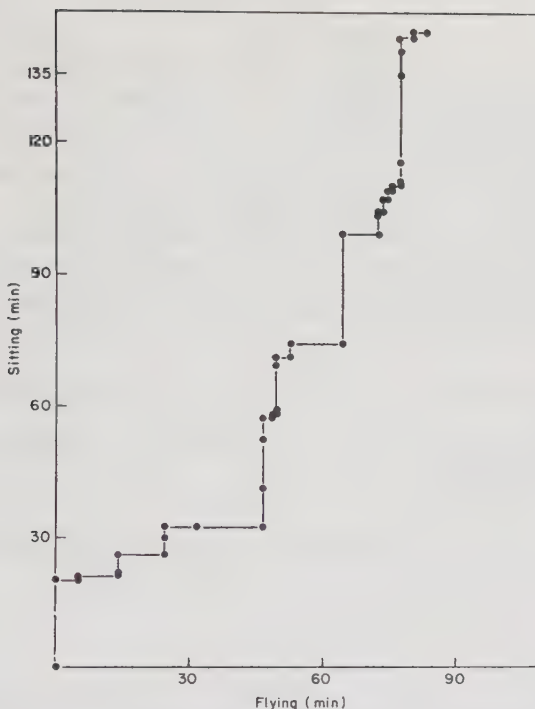


FIGURE 1. Cumulative pattern of activity of a Tawny Owl during a 3 h 45 min period in the night of 5 May 1975. The figure shows the sequence of events i.e., flying (horizontal lines) and hunting from a perch and resting (vertical lines). Black dots on vertical lines denote changing from one perch to another and dots on horizontal lines shows change of habitat.

Tawny Owl territories in Britain, studied by Southern (e.g., 1970), consisted almost exclusively of woodland. This may explain why these owls exclusively sought prey from perches. The British Tawny Owls had territories from 12 to 32 ha (Southern 1970). The home ranges of the owls in my study were estimated at 146 and 89 ha respectively, by means of the 'minimum area method' (Stickel 1954), i.e., the maximum area enclosed by all observations of hunting. However, small parts of their territories were not utilized over the duration of this rather brief survey (Nilsson 1977).

The energy expenditure of a Tawny Owl hunting on the wing is much higher than when it sits and waits for prey. Thus, if the availability of prey is similar in woods and open ground, a larger area providing more prey is perhaps needed when the home range consists mainly of open ground, especially dry ground, which probably is in fact less productive for Tawny Owls. The open marshes, in the Revinge area, supporting a large population of Field Voles *Microtus agrestis*, were extensively exploited in comparison with the other open habitats (Nilsson 1977). Smeenk's (1972) study area seems to be similar to mine, with small woods in an open landscape, so the difference in hunting behaviour between these two localities is hard to explain. Perhaps the open habitats differed in prey availability.

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THE PREY WEIGHT, FOOD OVERLAP, AND REPRODUCTIVE OUTPUT OF
POTENTIALLY COMPETING LONG-EARED AND TAWNY OWLS

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SUMMARY

(1) Food niches of two owl species, the long-eared owl Asio otus and the tawny owl Strix aluco, were compared. The niche breadth values of the tawny owl were about three times higher than those of the long-eared owl. Both species, however, utilized about the same number of prey categories.

(2) When utilizing the same area, the tawny owl took more water voles, birds, and amphibians and less field voles than did the long-eared owl.

(3) The mean prey weights for the two species were positively correlated in different seasons, and were equal or higher for the tawny owl during every season of the year.

(4) Both species took lighter prey than expected for their weights according to Schoener (1968); the deviation being largest for the tawny owl. Degree of food specialization is suggested as one reason for this deviation.

(5) Food overlaps were lower for neighbouring than for non-neighbouring owls. This indicates that the species compete for food.

(6) Food overlap was dependent on the sample size; smaller samples giving higher variation in the distribution of the overlap values.

(7) Reproductive output for long-eared owls increased with their distance to tawny owls. The opposite was found in tawny owls. The reason for this pattern in the long-eared owl is suggested to be competition for food, whereas the pattern in the tawny owl is suggested to be an effect of the fact that the long-eared owl settles in a tawny owl territory more probably, when it contains relatively abundant prey than when it doesn't. The probable effect of competition on the tawny owl is then not possible to establish in this analysis. However, the competition seems to be asymmetrical.

INTRODUCTION

Studies on the limiting similarity of co-existing species have changed from examining if their niches differ to how much they differ (Schoener 1974), and, to examining the effect of the overlap when two species occur in the same area (e.g. Högstedt 1980). In an extensive review, Schoener (1974) concluded that habitat is the most common niche segregating dimension, whereas food and time are important in some cases.

Contrary to previous results and suggestions (e.g. Southern 1954, Smeenk 1972, Delmée et al. 1979) extensive habitat overlap was found between the tawny owl (Strix aluco L.) and the long-eared owl (Asio otus L.) in a South Swedish open area (Nilsson 1978a). In this study I examine the food niche, food overlap, and reproductive output of these two owl species when inhabiting the same area. The aim is to find if neighbouring breeding pairs of tawny owls and long-eared owls tend to separate in diet compared to pairs exploiting different hunting grounds, and if neighbour breeding has any influence on reproductive success.

STUDY AREA AND METHODS

The diet of long-eared owls and tawny owls was examined in the Revinge area (about 4300 ha) in southern Sweden 1975-1976. The area is an open landscape with sandy hills, grazed fields, wet meadows, marshes, and small coniferous and deciduous woods. For details about the area see Nilsson (1981).

Pellets were collected from the roosts and the breeding places of the two owl species. Pellet samples produced by both species during the same periods were considered a sample pair. If owls of the two species had access to the same hunting area i.e. usually had roosts or nests within one kilometer of each other at the same marsh or meadow area, the preferred hunting ground (Nilsson 1978a), they were considered as neighbours. If, on the other hand, the probability that the two owl species hunted in the same areas was low, i.e. individuals of the two species were separated by more than two kilometers, and by the proximity to different wet areas (meadows and marshes), they were considered non-neighbours. Other samples were excluded.

The number of small mammal and bird prey individuals were estimated according to Nilsson (1981). The number of amphibians in a sample was estimated by counting pairs of tibiotarsus. This was the best estimator of amphibian numbers (Nilsson unpubl.). Birds were divided into seven weight classes for the analysis of prey weights. The prey weights were determined according to Nilsson (1981, Table 1). In addition, amphibian prey was estimated to weigh about 7.5 g (Nilsson unpubl., J. Loman pers. comm.). The following animal groups were taken as different prey categories; all mammalian species (except bats and lagomorphs which were each considered as one group), frogs (Rana sp.), toads (Bufo sp.), and the seven weight classes of birds.

Food niche breadth (NB) was estimated according to Levins (1968); $NB = (\sum p_i^2)^{-1}$, where p_i is the proportion of prey category i in the food. Food overlap was measured by the percentage similarity (PS); $PS = 1 - 0.5 \sum |p_{ji} - p_{ki}|$, where p_i is the proportion of prey species i in the diet of the predators j and k , respectively (Colwell and Futuyma 1971, Hanski 1978, Linton et al. 1981). Samples of less than 10 prey individuals were not used in calculations of niche breadth and overlap. Furthermore, in these calculations birds and amphibians were not divided into subgroups.

The location of pairs and individuals of both species were estimated from observations of territorial hooting, nests, and hunt-

ing or resting individuals. The number of young leaving the nests in 1974 and 1975 was used in the analyses of the possibility of a competitive effect on the reproductive output. A few nests, which failed due to human disturbance, were excluded.

RESULTS

Food and prey weight

The long-eared owl in the Revinge area fed mainly on field voles (about 70 % by numbers) and wood mice (about 15 %), whereas the tawny owl had a more varied diet consisting mainly of amphibians (about 30 %), field voles (about 20 %), wood mice (about 15 %), and birds (about 10 %) (Nilsson 1981 and unpubl.).

When the two species had access to the same hunting grounds the tawny owl took more water voles, birds, and amphibians than the long-eared owl. The latter prey category was not utilized at all by the long-eared owl (Table 1). The tawny owl took less field voles than the long-eared owl. Similar results were obtained by Källander (1977). There was no correlation between the proportion of these major prey categories in the diet of the two owls (Spearman's rank correlation, $p > 0.10$).

TABLE 1

Mean proportion of important prey in the diet ($\pm$ SD) of neighbouring tawny owls and long-eared owls (percentage of the prey individuals) calculated from 27 sample pairs.

Prey species	<i>Strix aluco</i>	<i>Asio otus</i>	Significance level in median test, one tailed
<i>Microtus agrestis</i> (L.)	22.6 $\pm$ 21.8	66.1 $\pm$ 23.7	$p < 0.001$
<i>Apodemus</i> sp.	11.1 $\pm$ 9.7	18.7 $\pm$ 15.0	n.s.
<i>Arvicola terrestris</i> (L.)	14.3 $\pm$ 13.0	8.6 $\pm$ 14.1	$p < 0.01$
Birds	20.1 $\pm$ 13.3	3.2 $\pm$ 5.7	$p < 0.001$
Amphibians	30.6 $\pm$ 20.8	0	$p < 0.001$

Median prey weights of neighbouring owls were positively correlated (Fig. 1), as were mean prey weights ($r_s = 0.63$, $p < 0.01$). The latter correlation was also present if amphibians were excluded i.e. only prey in common compared ($r_s = 0.53$, $p < 0.02$).

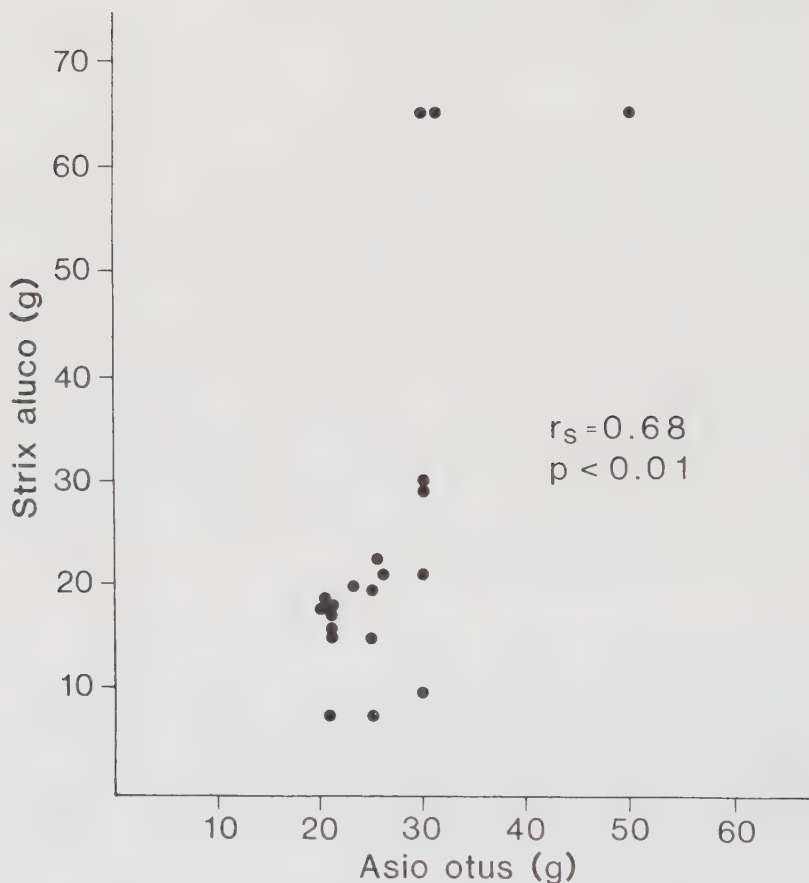


Fig. 1. Correlation between the median prey weights (g) of neighbouring long-eared owls and tawny owls.

Median prey weights were on average about 29 g for the long-eared owl and 32 g for the tawny owl.

Median prey weights were higher for the long-eared owl during the periods Jan - Apr and Sep - Dec (Median test, one-tailed, $p < 0.05$ and $p < 0.001$, respectively), whereas there was a tendency for the tawny owl to have higher median prey weights during the period May - Aug. This, however, was not statistically significant ($p > 0.05$).

Mean prey weights for the tawny owl tended to be higher than those of the long-eared owl during all three seasons (see above), as was the case for the whole year (Table 2). These differences, however, were not statistically significant. If amphibians are excluded these differences were statistically significant for the whole year (median test, one-tailed, $p < 0.01$), for the period Jan - Apr ($p < 0.02$), and almost so for May - Aug ($p = 0.07$).

TABLE 2

Mean prey weight in the diet (g; weighted according to the number of prey in the 27 different sample pairs) of neighbouring tawny owls and long-eared owls. The number of prey individuals are given in parenthesis.

Period	Strix aluco		Asio otus
	All vertebrates	Amphibians excl.	
Jan - Apr	33.8 (118)	45.8 (81)	25.7 (1398)
May - Aug	52.3 (222)	64.4 (175)	41.7 (342)
Sep - Dec	21.3 (307)	31.3 (177)	21.4 (3932)
Whole year	34.2 (647)	47.4 (433)	23.4 (5732)

Both species exploited a similar number of prey categories; highest for the tawny owl during the summer and for the long-eared owl during autumn (Table 3).

TABLE 3

The number of prey categories in the food of neighbouring tawny owls and long-eared owls. Birds were divided into seven weight classes.

Period	Strix aluco	Asio otus
Jan - Apr	12	12
May - Aug	17	12
Sep - Dec	15	14
Whole year	20	16

The great differences in food niche breadth (Table 4) between the two owls were due to the concentration on few prey species in

TABLE 4

Food niche breadth for neighbouring and non-neighbouring tawny owls and long-eared owls. The samples were combined for each species and year to be comparable. Birds were taken as one group. The number of prey individuals is given in parenthesis.

Year	Neighbouring owls		Non-neighbouring owls	
	Strix aluco	Asio otus	Strix aluco	Asio otus
1975	5.14 (257)	1.83 (1144)	4.87 (609)	1.86 (980)
1976	4.51 (73)	1.32 (638)	5.21 (511)	1.52 (869)
Both years combined	5.07 (330)	1.63 (1782)	5.13 (1120)	1.70 (1849)

the long-eared owl (Table 1, Nilsson 1981), and the relatively even distribution on several prey species in the tawny owl (Table 1, Nilsson unpubl.).

The food niche breadth of the two owls showed small changes between the two years, both with and without the other species present (Table 4).

Median prey weight was positively correlated with the niche breadth for the long-eared owl (Spearman's rank correlation, $p < 0.01$), whereas no such correlation was found for the tawny owl ($p > 0.10$). This is due to the fact that, when increasing their food niches, the long-eared owl takes more of the larger prey such as water voles and starlings (*Sturnus vulgaris* L.), whereas the tawny owl takes more of both large and small prey. Median prey weight was positively correlated with the food overlap for the tawny owl ($p < 0.025$), but not for the long-eared owl ($p > 0.10$). No correlation between niche breadth and overlap was found ($p > 0.10$).

Food overlap tended to change during the year, being greater during the summer than during the rest of the year (Table 5). This difference, however, was not statistically significant (Mann-Whitney U test, one-tailed, $p > 0.05$). The food overlaps for neighbouring owls were smaller than the average for non-neighbouring owls in the Revinge area and for the owls in different European regions (Table 6, Mann-Whitney U test, one-tailed, $p = 0.012$). Also, the food overlap of neighbouring owls was smaller when tested against all possible sample pairs

TABLE 5

Seasonal changes in food overlap in neighbouring tawny owls and long-eared owls (mean for each season). The number of sample pairs are given in parenthesis.

Season	Overlap $\pm$ SD
Jan - Apr	0.30 $\pm$ 0.13 (6)
May - Aug	0.41 $\pm$ 0.09 (7)
Sep - Dec	0.34 $\pm$ 0.11 (8)

(produced during the same time) of non-neighbouring owls (Mann-Whitney U test, one-tailed, $p < 0.05$).

When overlap was plotted against the number of prey individuals in the smallest sample in the pair (Fig. 2), overlap indices were not independent of sample size; the smaller the sample, the larger the variation. Similar results were recently obtained by Linton et al. (1981). This indicates that caution should be taken, regarding sample size, when calculating overlap.

Reproductive output

Non-neighbouring long-eared owls and neighbouring tawny owls tended to have higher numbers of young leaving the nests (Table 7; t-test, $0.10 > p > 0.05$). In the long-eared owl the number of young leaving the nest increased with the distance to the nearest nest, or territory center in a few cases, of the tawny owl (Fig. 3). The opposite was the case for the tawny owl in relation to the nearest nest of the long-eared owl (Fig. 4).

TABLE 7

Reproductive output (number of young leaving the nest $\pm$ SD) in neighbouring and non-neighbouring long-eared owls and tawny owls. Sample size is given in parentheses.

Neighbouring owls		Non-neighbouring owls	
Asio otus	Strix aluco	Asio otus	Strix aluco
2.6 $\pm$ 1.3	3.3 $\pm$ 1.0	3.5 $\pm$ 0.5	2.3 $\pm$ 0.8
(10)	(7)	(8)	(10)

TABLE 6

Food overlap between neighbouring and non-neighbouring Latvian owls and long-eared owls in the Revinge area, and between the same owl species in different regions of Europe. The latter overlap values were calculated from data in Smeenk (1972, Tables 8 and 9), Weber (1973, Table 1), Källander (1977, Tables 1 and 2), Delmée et al. (1979, Table 4), and the mean value for this study.

	R e v i n g e a r e a		E u r o p e
	Neighbouring owls	Non-neighbouring owls	
Overlap $\pm$ SD	0.35 $\pm$ 0.12	0.46 0.42 $\pm$ 0.13	0.51 $\pm$ 0.19
Number of samples	21 sample pairs	27 samples for Asio otus and 42 for Strix aluco; combined for each species. 14 non-neighbouring samples of each species; paired if produced during the same time.	11 sample pairs

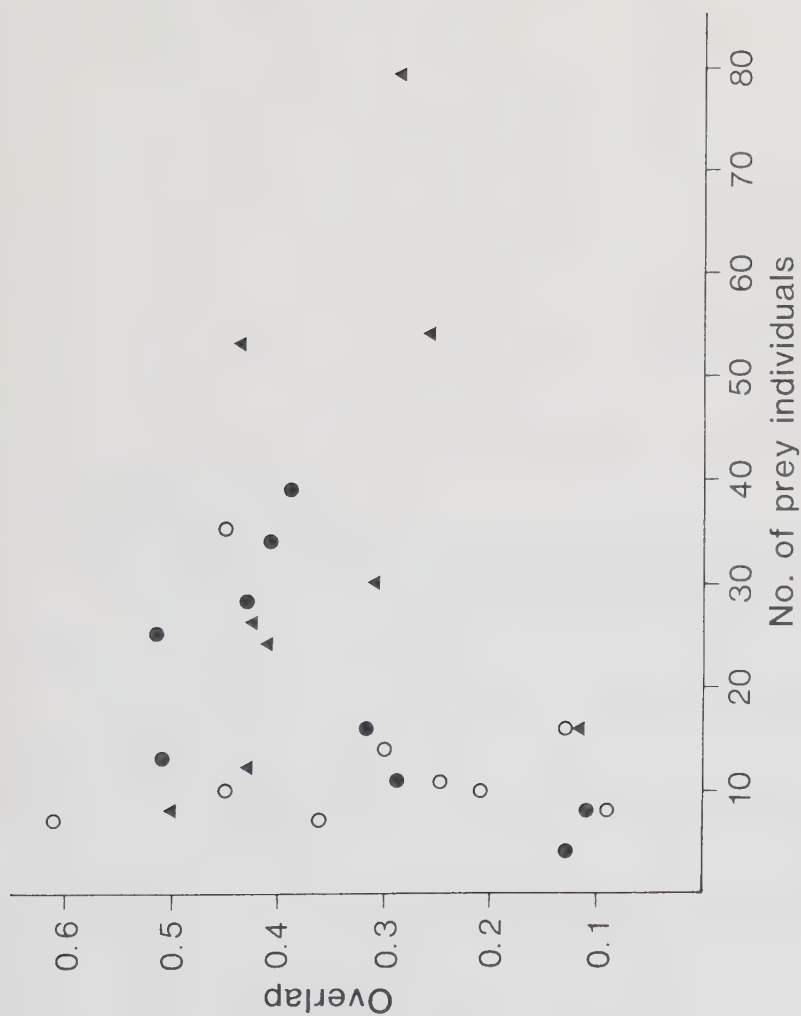


Fig. 2. The effect on the overlap index of the smallest number of prey individuals in a sample pair comparing the diet of neighbouring long-eared owls and tawny owls. Seasons are indicated as follows: O = Jan - Apr, ● = May - Aug, and ▲ = Sep - Dec.

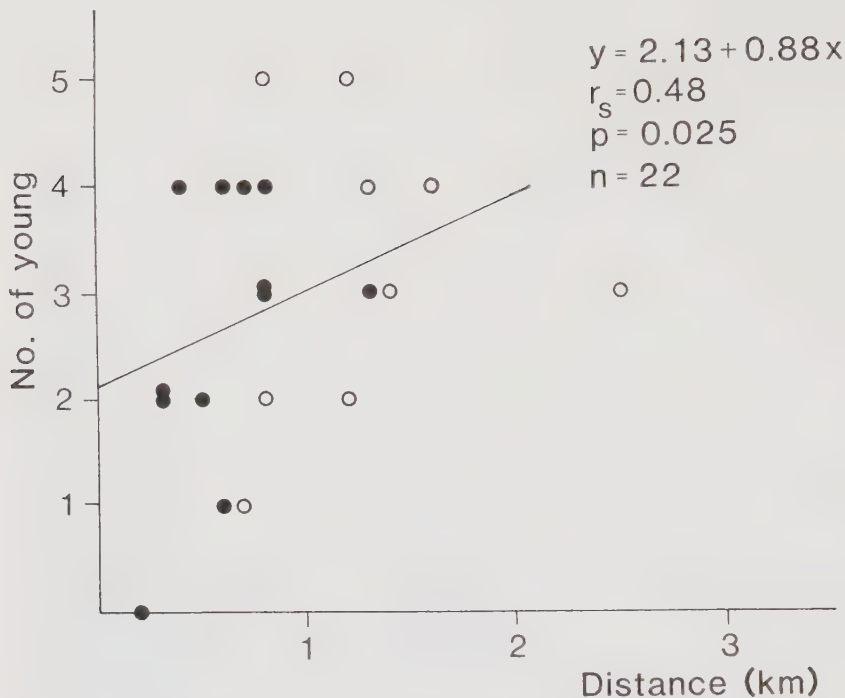


Fig. 3. Reproductive output (young leaving the nest) in the long-eared owl as a function of the distance to the nearest nest of the tawny owl. The symbols refer to two different years.

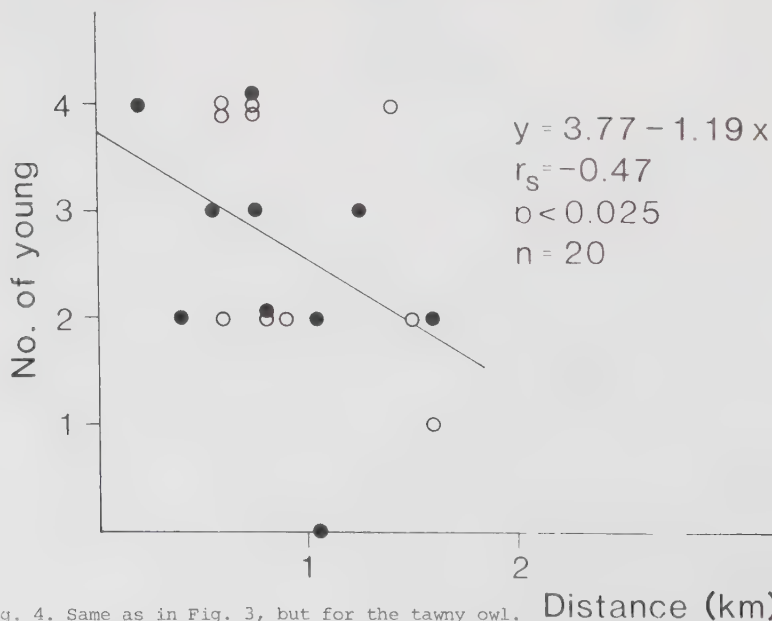


Fig. 4. Same as in Fig. 3, but for the tawny owl.

TABLE 8

Observed mean prey weights (g , given in Table 2) in relation to that predicted by the mean prey weight of the other species, using the regression slope given by Schoener (1968) for a regression of log prey weight on log predator weight for raptorial birds. The long-eared owl is supposed to weigh 276 g and the tawny owl 472 g (Hartorn 1971).

If also the intercept in Schoener's (1968) regression is used, much higher values are obtained (given in parenthesis).

	A s i o o t u s			S t r i x a l u c o		
	Predicted	Observed	Difference	Predicted	Observed	Difference
Jan - Apr	20.5	25.7	+ 5.2	42.3	33.8	- 8.5
May - Aug	31.8	41.7	+ 9.9	68.7	52.3	- 16.4
Sep - Dec	13.0	21.4	+ 8.4	35.2	21.3	- 13.9
Whole Year	20.8 (54.0)	23.4	+ 2.6 (- 30.6)	38.5 (89.0)	34.2	- 4.3 (- 54.8)

DISCUSSION

Why do the long-eared and tawny owls feed on similar sized prey?

The long-eared owl and the tawny owl are sympatric in many areas in Europe. The former species weighs about 275 g and the latter about 475 g (Haftorn 1971. This difference in size indicates that they should separate by feeding on different-sized prey (e.g. Storer 1966, Schoener 1968); the tawny owl taking larger prey than the long-eared owl (see also Hespenheide 1975). There was a tendency for this during late winter through summer in the mean prey weights (Table 2). However, during the autumn and early winter the owl species had the same mean prey weights, and during autumn to spring the long-eared owl had higher median prey weights, which is the opposite of the prediction. If only prey categories in common were compared, i.e. amphibians excluded, the prediction was verified during all seasons as concerns mean prey weight (Table 2). If the observed mean prey weights are compared with the expected ones (Table 8), using the regression slope calculated by Schoener (1968) for raptorial birds, the same pattern occurs during every period for each owl species (see also Hespenheide 1971); the long-eared owl takes larger prey than expected and the tawny owl smaller prey than expected, especially so during the summer. However, if the intercept of Schoener's (1968) regression equation is also used both species take much lighter prey than predicted, the tawny much more so than the long-eared owl. This indicates either that the regression line (intercept) is too high for owls, as also Hespenheide (1971) concluded, or that the regression slope is less steep for owls than for other raptorial birds. A combination of both explanations is also possible. Another possibility is, that the prey size distributions on the continents are different. This, however, I consider less probable (see also below). The slightly different hunting methods, the long-eared owl hunting more on the wing, could also result in similar prey weights (Hespenheide 1973).

The tawny owl is a more generalized predator than the long-eared owl (Table 1). However, the latter also preys a large number of prey categories (Table 3); almost as many as the tawny owl. This similarity is difficult to explain in terms of optimal foraging theory (e.g. Pyke et al. 1977), which predicts that a feeding specialist should take few prey categories. Nilsson (1981) suggested e.g. diffuse competition, habitat sampling

(Pulliam 1974), and opportunistic hunting in selected patches (Royama 1970) as the most probable explanations. There are, however, still other possible explanations which arise when comparing the two owl species. The tawny owl is a resident and territorial species (e.g. Southern and Lowe 1968) and the long-eared owl is a migrant (at least partially) without hunting territory. The latter hunts over an area at least four times larger than that of the tawny owl (Nilsson 1978b and unpubl., H. Wijnandts pers. comm.). The tawny owl, besides taking larger prey such as water voles, also depends on smaller prey such as amphibians. The long-eared owl, besides usually taking smaller prey, primarily field voles, also takes larger prey such as water voles and starlings, especially during breeding time (Nilsson 1981). The similarity in prey size can be explained, at least partly, in the light of central place foraging theory (Orians and Pearson 1979, Schoener 1979). The tawny owl mostly uses a sit-and-wait strategy (Nilsson 1978b), whereas the long-eared owl hunts on the wing. Then, the total travelling cost for the tawny owl is low, compared to that of the long-eared owl, and, therefore, the tawny owl can exploit populations of smaller prey relative to its size. The long-eared owl, on the other hand, has a much higher travelling cost, especially so during the breeding season with increased food demands, and thus has to take larger and larger prey the more it has to increase its hunting area, to be efficient. This could be a reason for the deviation from the expected size-related prey weights (Table 7, see also Hespenheide 1973). Thus, I hypothesize that 1) a specialization on fewer food types leads to an increased hunting area, compared to that of generalist predators and omnivores (Schoener 1968), 2) this increases the travelling costs (including search time), and 3) promotes a tendency to take relatively larger prey, when food demand increases or prey availability decreases, compared to an equal-sized less specialized predator. The advantage of specialization on small prey species is then counter balanced by increased travelling costs. Another important factor is, probably, the degree of prey predictability in the habitats. However, few, if any, specialized vertebrate predators have lost the ability to switch temporarily to other food types when the abundance of their staple prey species is low. The long-eared owl e.g. has up to 80 % birds in its diet in some cases (Tinbergen 1933).

Competition between long-eared and tawny owls

If the two owl species don't have any effect on each others food spectrum, i.e. no food competition occurs, food overlap for samples of neighbouring owls should be similar to or, more probably, higher than overlap values for non-neighbouring owl pairs, as there is a higher probability for neighbouring owl pairs than for non-neighbouring pairs to exploit similar prey populations. However, the overlaps of neighbouring owls were lower than for non-neighbouring ones (Table 6). This, I believe to be an effect of food competition between the two owls. The same conclusion was drawn by Colwell and Futuyma (1971) in their discussion of actual and virtual niche breadth and overlap.

The importance of competition, in terms of reduced fitness, is usually difficult to assess (e.g. Lawlor 1980 with references). However, Högstedt (1980) showed that one species (jackdaw, Corvus monedula L.) reduced the reproductive output of another one (magpie, Pica pica L.). This study showed the same result for the tawny owl in comparison with the long-eared owl (Table 7, Fig. 3), which showed that competition for food probably affected the reproductive output. However, the opposite correlation was found in the tawny owl (Table 7, Fig. 4). How can this be explained? The reason is probably the following. Long-eared owls redistribute each year presumably mainly in relation to the local food abundance. Tawny owls, on the other hand, remain in the same area for several years (e.g. Delmée et al. 1978). Thus, when a pair of tawny owls have a high abundance of prey in their territory, a certain year, it is more probable that a pair of long-eared owls establish themselves in that vicinity. The expected negative effect, on the reproductive output of tawny owls, could then not be measured with the methods used. However, it seems clear that the tawny owl has a more severe effect on the reproductive output of the long-eared owl than the opposite.

What, then, are the forms of this competition? Three mechanisms are possible: food exploitation, interference, and resource depression by behavioural and/or micro-habitat changes of the prey species (Charnov et al. 1976). The small mammal populations in the Revinge area are exposed to continuously high predation by many predators; common buzzard (Buteo buteo (L.)), red fox (Vulpes vulpes (L.)), and domestic cat (Felis catus L.) having the highest impact (Erlinge et al. unpubl.). Therefore, it seems probable that, due to diffuse competition (MacArthur 1972), the

two owls are faced with a shortage of food during most of the year. It is thus probable that the food exploitation component, in the competition between the two owls, is of relatively little significance.

There are a few records of interference ("combats") between the two owls (Nilsson 1978a with references). The appearance of an owl when another is hunting might also reduce the latter's chances of finding a prey due to distraction. Also, the tawny owl, as the larger species, could displace the long-eared owl, at least temporarily, from a utilized patch (Nilsson 1978a). This could explain the suggested asymmetric effect of competition.

The effect of a predator on the behaviour and microdistribution of the prey is another mechanism in competition (Charnov et al. 1976). This could be equally important to the two owls, particularly for hunting success on more agile prey such as birds, mostly preyed upon during breeding time (Nilsson 1981), as the two owls spend much of their time hunting on the wing (Nilsson 1978a and b, H. Wijnandts pers.comm.). These mechanisms could result in the two owls hunting temporarily in different localities (Charnov et al. 1976), giving the observed overlap patterns for neighbouring and non-neighbouring owls. Other predators in the area could possibly also have an effect on the availability of prey. Usually, however, they are segregated from the owls by time and/or habitat (Erlinge et al. unpubl.). One species that could be of some importance in this respect is the stoat, Mustela erminea L., as it has a similar habitat preference and also hunts to some extent during the night (Erlinge 1981 and unpubl.).

In conclusion, the two owl species that usually, in relation to their total populations, are in a non-competitive situation to each other, can locally, and perhaps also due to human habitat alteration, come into competition. This situation perhaps occurs more often than is usually suggested. The evolutionary outcome of such a situation could be a restricted habitat preference and broadened food niche for the inferior species, in this case the long-eared owl (see also Partridge 1978, Schoener 1969).

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PREY CHOICE, RESOURCE DEPRESSION, AND THE REGULAR NEST

SPACING OF BIRDS OF PREY

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ABSTRACT

The hypothesis is suggested that resource depression is one important factor behind the observed regular nest spacing of most birds of prey. It predicts that the proportion of evasive prey in the predators diet should be reflected in the degree of regularity in its nest spacing. It is tested on data from 24 raptorial bird populations of 19 species. The proportion of supposed evasive prey (birds and large mammals) in the diet was positively correlated with the degree of regularity in spacing of the nests, considering all populations or species. No such significant correlation was found for the six highly territorial species, whereas the correlation was highly significant for the other 13 species. Thus, the hypothesis seems then applicable only to species with widely overlapping homeranges. However, resource depression could be one reason for the evolution of territoriality.

INTRODUCTION

Breeding dispersion of raptors is normally governed by the distribution of food and/or nest sites, and particular dispersion patterns are not necessarily species-specific (Newton 1979). There are numerous examples of species adopting different systems according to how the food is distributed. The regular nest spacing of raptorial birds has, however, been emphasized by several authors (e.g. Cade 1960, Ratcliffe 1962, Newton 1976, Newton et al. 1977, Newton 1979). Generally, regular nest spacing among birds has been explained in two ways (review by J.L. Brown 1976). Firstly, if food is evenly distributed and fairly stable, travelling time is minimized if the nests are regularly spaced (Horn 1968, Newton 1976, 1979). Secondly, some authors suggest that nest predation acts as a selective force against clumped nests. Density dependent predation on nests has been demonstrated (Tinbergen et al. 1967, Krebs 1971, Fretwell 1972, Göransson et al. 1975, Andersson and Wiklund 1980) but seems unlikely to prevail among raptorial birds as they usually breed at very low densities (Newton 1979). Even the first hypothesis does not, in our opinion, explain the variability of nest spacing. To account for this variability we suggest a new hypothesis based on the idea of "resource depression" (Charnov et al. 1976).

HYPOTHESIS

The appearance of a predator may reduce the availability of its prey (Rudebeck 1950-51, Goss-Custard 1970, 1980, Charnov et al. 1976). Such reactions by birds, through e.g. warning calls and mobbing of predators, are common knowledge (e.g. Curio 1975). "The golden eagle,, is said to clear a moore of grouse

if it appears in the sky, and a good day's driving is spoiled" (L. Brown 1976, p. 302). The proportion of time used scanning for predators increased after the appearance of a potential predator (Caraco et al. 1980). Even a mouse, Peromyscus maniculatus, reacts on the presence of a ground predator, by being more stationary (Hirsch and Bolles 1980).

We suggest that one reason why raptors space their nests regularly is because of resource depression (Charnov et al. 1976). Since the hunting areas of nearby pairs of many raptor species overlap (Newton 1976, 1979), the chance that individuals from different pairs hunt in the same area at the same time is minimized if the nests are as far apart as possible, at any given density. Since all neighbours benefit from a regular nest dispersion, it is in the "interest" of all pairs that such a pattern is achieved. The aerial displays by diurnal raptors and the calls of nocturnal ones, i.e. mainly owls, can provide the necessary proximate mechanism. Because of the mutual benefits to unrelated birds the behaviour could arise through individual selection.

We argue that the ability of the raptors' prey to detect and react evasively to an approaching predator at a distance should to some extent be reflected by the degree of regularity of the raptors' nest spacing. Due to lack of systematic observations on evasive behaviour we find it difficult to make more precise predictions at the moment. However, prey in open habitats and/or moving off the ground seems most likely to have the ability of evasive reactions, as do probably larger prey species. Thus, birds and larger mammals, e.g. a ground squirrel (Balph & Balph 1966), can probably react such that the predators experience resource depression when hunting for them. This lowering of the prey availability is governed by changes in behaviour and/or microhabitat of evasive prey. Thus, we predict that aerial predators hunting for evasive prey should space their nests more regularly than predators hunting for e.g. small rodents.

Although Hirsch and Bolles (1980) showed that Peromyscus reacted to the presence of some ground predators, this ability is probably of less importance in field situations, especially considering flying predators. We have used these considerations in a preliminary test of the hypothesis, comparing the food composition of some raptors with the regularity of their nest spacing.

MATERIAL AND METHODS

The regularity of nest spacing was measured by the G-statistic (GMASD) suggested by Brown (1975) and further elaborated by Brown and Rothery (1978). G-values from zero to about 0.65 indicate randomness, and above that, up to one, increasing degree of regularity. Data on food and the distribution of at least 10 nests per study area was extracted from the literature, complemented with unpublished results from other sources. In those six cases, when information on both food and nest dispersion was not available from the same area, food data from nearby areas was used. As large mammals we have considered species the size of a squirrel or larger (≥ 200 g).

RESULTS

The G-values ($\pm$ SD) for the raptorial bird populations studied varied between 0.40 and 0.93, and averaged 0.77 ($\pm$ 0.13, Table 1). There was a positive correlation between the proportion of larger mammals and birds in the diet and the degree of regularity of nest spacing (Fig. 1). When considering these two prey categories separately, no such significant correlations were found ($p > 0.10$).

Considering the species means ($n = 19$) similar results were obtained ($G = 0.76 \pm 0.13$; regression line $y = 0.64 + 0.0023x$, $r = 0.62$, $p < 0.01$).

There was an inverse correlation between the proportion of small mammals (populations with more than one % in the diet) and the G-value ($n = 18$, $r = -0.71$, $p < 0.001$), probably as a result of the inverse correlation between the proportion of small mammals and the proportion of birds and large mammals together ($r = -0.91$, $p < 0.001$) in the diet.

Mean species weight of the raptorial birds (Cramp and Simmons 1980, Glutz and Bauer 1980) was positively correlated with the mean nearest nest distance, a measure of home range size (Table 1, $r = 0.71$, $p < 0.001$), as earlier shown for diurnal raptors (Newton 1979).

A tendency for a positive correlation was found between the proportion of large mammals and birds together in the species' diets and the mean nearest nest distances (Table 1, species means; $r = 0.41$, $p < 0.10$). No significant correlation was found between the G-value and the mean nearest nest distance of the species ($p > 0.10$).

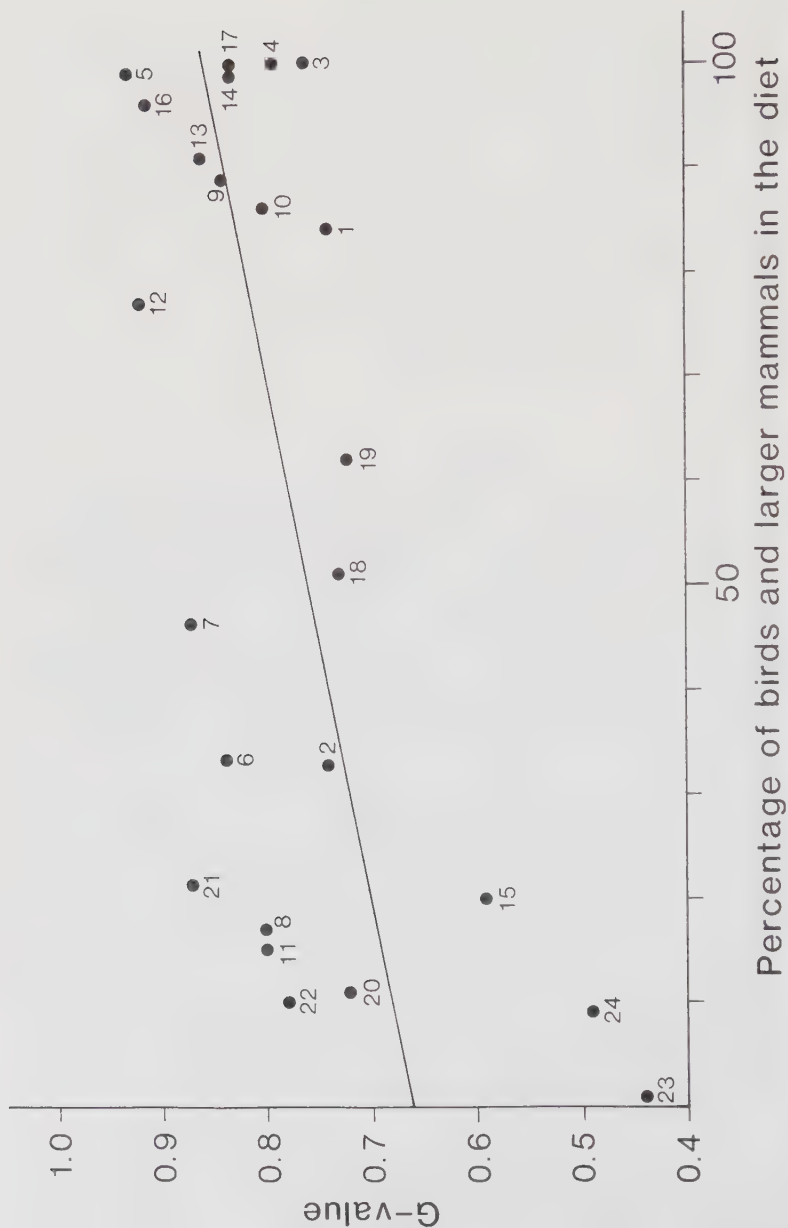


Fig. 1. The correlation between the proportion of birds and larger mammals (≥ 200 g); both % by numbers) and the regularity of nest spacing (measured by the G-value according to Brown 1975). The regression line is $y = 0.67 + 0.0019x$ ($r = 0.57$, $p < 0.01$, $n = 24$).

TABLE 1

Data on some populations of birds of prey. When the number of nests is given as a range it means the number of nests in one area during different years, or from different areas in the same study. Food choice during breeding time only is given. Food proportions less than one percent are indicated (+). Where data on nest spacing (n) and food (f) was obtained from different sources this appropriately is indicated.

Species	Area	Popu- lation No. on Fig. 1	Excl. hunting terri- tories	No. of nests	G-value	Food composition (% by numbers)						Species' mean nest dist- ances (km)	Data source
						Birds	Larger mammals	Small mammals	Reptiles and amphi- bians	Fish	Others		
<i>Milvus milvus</i>	Sweden	1	-	33	0.74	76	8	10	-	6	-	3.0	M.Sylvén unpub.
<i>Circus aeruginosus</i>	"	2	-	24	0.74	29	4	55	6	2	4	0.5	T.Persson unpub.(n) Giutz et al.1971(f)
<i>Accipiter gentilis</i>	Finland	3	-	19	0.76	90	10	-	-	-	-	4.8	H.Pietiläinen unpub.(n), Sulkava 1964(f), Wikman & Tarna 1980(f)
"	Germany	4	-	27	0.79	95	5	-	-	-	-		Brüll 1977 (n) Opdas 1975 (f)
<i>Accipiter nisus</i>	UK	5	-	13-121	0.93	98	1	1	-	-	-	1.2	Newton et al. 1977
<i>Buteo lineatus</i>	USA	6	X	18-21	0.84	29	4	30	37	-	-	1.2	Craighead and Craighead 1969
<i>Buteo jamaicensis</i>	USA	7	X	19-21	0.87	30	16	43	8	-	1	1.5	Petersen 1979
<i>Buteo buteo</i>	Germany	8	X	17-42	0.80	12	5	68	18	-	-	1.8	Mabe 1964
"	Sweden	9	X	17	0.84	19	70	10	1	-	-		M.Sylvén unpub.
"	UK	10	X	22	0.80	79	7	14	1	-	-		Tubbs 1976
"	Finland	11	X	13	0.80	14	1	54	25	-	7		H.Pietiläinen unpub. (n), Soumas 1953(f)
<i>Aquila chrysaetos</i>	UK	12	-	16	0.92	23	54	23	-	-	-	10.7	L.Brown 1976
"	Sweden	13	-	16-21	0.86	66	25	1	-	-	8		M.Tjernberg 1981 and unpub.
<i>Aquila verreauxi</i>	Rhodesia	14	X	17-18	0.83	+	100	-	+	-	-	2.6	Gargett 1975,1977
<i>Falco tinnunculus</i>	Sweden	15	-	11	0.59	20	-	78	2	-	+	1.0	G.Böystedt unpub.
<i>Falco subbuteo</i>	"	16	-	21	0.91	95	-	5	-	-	+	3.9	M.Cornert unpub.
<i>Falco peregrinus</i>	UK	17	-	15	0.83	100	-	-	-	-	-	4.5	Ratcliffe 1962
<i>Bubo bubo</i>	Sweden	18	-	20	0.73	45	6	45	2	2	+	8.5	Olsson 1979
<i>Bubo virginianus</i>	USA	19	-	11-12	0.72	43	19	36	+	-	+	2.3	Petersen 1979
<i>Athene noctua</i>	Netherlands	20	-	24-33	0.72	10	+	30	+	-	60	1.7	P.Fuchs unpub. (n), Thiollay 1968 (f), Tinbergen and Broek- huysen 1934 (f)
<i>Strix aluco</i>	Sweden	21	X	13	0.87	19	2	44	35	-	+	1.5	I.Nilsson unpub.
<i>Strix uralensis</i>	"	22	X	28	0.78	8	2	86	3	-	-	1.2	A.Lundberg 1976 and unpub.
<i>Strix nebulosa</i>	"	23	-	11	0.40	1	+	99	-	-	-	3.6	O.Stefansson unpub. (n), Höglund and Lansgren 1968 (f)
<i>Asio otus</i>	"	24	-	12-21	0.49	9	+	90	-	-	+	1.3	I.Nilsson 1981 and unpub.

DISCUSSION

Clumped prey are probably most efficiently exploited by predators foraging in groups (e.g. Ward 1965, Horn 1968, Davidson 1977). Group foraging and colonial nesting have also been established for several raptorial birds (see e.g. Lack 1968, Newton 1979), mostly species feeding on carrion or insects, but also in a bird specialist like Falco eleonora, which, however, subsists on a continuous flow of migrating passerines during the nesting period (Walter 1979).

Some species deviate from their expected nest distributions. Milvus milvus (Fig. 1, dot No. 1) has a large proportion of birds in its diet. However, many of these are taken as recently fledged juveniles (Sylvén 1980, Davies and Davies 1981), and probably have little ability to react evasively on the presence of a predator. Furthermore, data on its nest dispersion was obtained from a region where nesting is mostly restricted to old beech trees, Fagus sylvatica, a limited resource in some parts of the area.

Two of the four Buteo buteo populations studied (8 and 11) have very regular nest dispersions in relation to their diet, indicating that nest spacing in this highly territorial species (see below) is not adjusted to the local food situation. Like B. buteo, B. lineatus (6) and B. jamaicensis (7) are also highly territorial. The two owls Strix aluco (21) and S. uralensis (22), which both have more regular nest distributions than expected, are also highly territorial.

The ability of fish to react evasively on the presence of a flying predator is unknown. However, if this ability can be shown also Pandion haliaetus, an exclusive fish eater, would fit the hypothesis ($G = 0.79$ for 17 - 23 nests; I. and S. Nilsson unpubl.).

There are several problems connected with a test of the hypothesis. Firstly, it is difficult to discriminate between the three types of intraspecific competition: interference, exploitation, and resource depression (Pianka 1974, Charnov et al. 1976). All the three are likely to produce spacing out of the nests. Interference, e.g. nest defence, is most intense in the vicinity of the nest and decreases rapidly with the distance from the nest (Newton 1979). Therefore, interference is probably not responsible for the much larger neighbour distances observed (Table 1). The effect of exploitation and resource depression on the nest distribution could be very similar. If the nests are situated centrally in the hunting areas (Orians and Pearsson 1978), and

these areas are contiguous a regular spacing of the nests would occur. Food depletion due to exploitation decrease with increasing distance from the central place (Andersson 1978), and this probably also concerns resource depression effects. To be able to separate between the effects of exploitation and resource depression detailed field studies are needed. However, it is difficult to explain the varying degree of nest spacing solely as an effect of exploitation.

Secondly, interspecific competition might influence nest distribution of a species in some cases, i.e. giving less regular intraspecific nest distributions than expected from the diets, and thus causing deviations from the hypothesis in some instances. Nest distribution in an area in Finland with both Strix aluco (8 pairs) and S. uralensis (13 pairs) breeding (H. Pietiäinen unpubl.) shows a lower G-value (0.65) for S. aluco alone, than when also S. uralensis nests were considered (0.91). These two species have very similar ecology (Lundberg 1980).

Thirdly, the availability of suitable nest-sites is another important factor, delimiting the pairs' possibilities of nesting in the central place (see Newton 1979 for a discussion). Such deviations can also result in less regular nest distributions than predicted by the hypothesis. Accipiter nisus (5) probably has less specialized requirements on the nest trees than has A. gentilis (3 and 4). Both species have a large proportion of birds in their diets but the former species can probably easier find a nest tree in the center of its hunting area as maybe indicated by the G-values, respectively.

Fourthly, the degree of territoriality is important. Nesting territories and hunting home ranges occur in most raptors but some species have mutually exclusive all-purpose territories (Newton 1979). The latter is likely to produce regular nest distributions in homogenous areas irrespective of the diet. This is also observed: the mean G-value being 0.83 (± 0.04) for highly territorial species and 0.73 (± 0.16) for other species (Table 1; t-test, $p < 0.05$). Furthermore, the correlation between the proportion of supposed evasive prey species (birds and larger mammals) and the G-value is weaker for highly territorial species ($r = 0.11$, $n = 6$, $p > 0.10$) than for other species ($r = 0.83$, $n = 13$, $p < 0.001$). Thus, it seems as if the proposed hypothesis is applicable mainly to species with widely overlapping home ranges. However, it could be argued that, for species with lim-

ited food resources during the breeding, resource depression could be one reason for the evolution of territoriality.

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The reversed size dimorphism in birds of prey: a new hypothesis

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With respect to egg laying, all female birds benefit from being large. Non-passerines benefit more than passerines. In species which make many provisioning trips, large sized birds are for bioenergetic reasons selected against. In birds of prey, the selective force favouring large females is united to the selective pressures acting on an increased provisioning efficiency, i.e. the need to transport large prey. Small male birds of prey on the other hand benefit from their greater hunting efficiency on small sized prey which hence enhances the reversed dimorphism.

The question why female birds of prey^a in general are larger than males has been raised several times (Amadon 1959, Storer 1966, Reynolds 1972, Newton 1979). Raptors that catch large prey in relation to their own body size, or those which feed mainly on birds, are more dimorphic than those that prey upon small or less fast-moving prey (Storer 1966, Brown and Amadon 1968, Earhart and Johnson 1970, Reynolds 1972, Snyder and Wiley 1976, Newton 1979). So far nobody has been able to explain these relationships satisfactorily (Newton 1979).

When sexual dimorphism in size occurs in birds, males are often larger than females. This has been explained by intrasexual competition (Trivers 1972), i.e. the males compete for females (Trivers 1972) or for territories that contain resources essential for reproduction (Emlen and Oring 1977). Species with males considerable larger than females are often polygynous (Lack 1968). As birds of prey in general are monogamous (Brown and Amadon 1968, Newton 1979), the intrasexual competition hypothesis does not explain why

females in many of these species are considerable larger than males (no correlation between breeding system and degree of dimorphism) (see also Ralls 1977), nor does it explain the link between diet and dimorphism (Storer 1966, Brown and Amadon 1968, Earhart and Johnson 1970, Reynolds 1972, Snyder and Wiley 1976, Newton 1979). Some authors (Storer 1966, Earhart and Johnson 1970, Newton 1979) have associated this latter observation to Selander's (1966, 1972) finding that sexual dimorphism may reduce intraspecific competition for food. Newton (1979) suggested that as fast-moving prey are exploited by very few predators, each such predator would have a wider niche, and more scope for within-species niche segregation than predators that feed on slow-moving and more intensively utilized prey. However, if size dimorphism in predatory birds purely is an adaptation to niche segregation, one might expect that island populations which are subject to competitive release (Cody 1974) should be more dimorphic than mainland populations. There is no support for this in the data of Brown and Amadon (1968). In addition, the niche segregation theory does not explain why female birds of prey are larger than males, which is the opposite for birds in general.

a. Falconiformes (hawks, eagles, etc.), Strigiformes (owls), and Stercorariidae (jaegers and skuas).

Recently, Ralls (1976) suggested that in mammals, the demands of pregnancy and lactation can be major selective forces determining the size of the females. In this paper we assign Ralls (1976) view to birds of prey and conclude that large female size both reduces the relative cost of egg production and enables the female to provide large prey to the young. The hypothesis explains both the direction and the degree of the dimorphism.

In birds, large egg size has been shown to be important for the viability of the chicks (Parsons 1970, Schifferli 1973). Accordingly, one obvious benefit for large females is their greater ability to lay large eggs (Loman 1980). We conclude, that for "central place" foraging birds (Orians and Pearson 1978), i.e. nidicolous species (species where the chicks can not feed by themselves but the parents have to provision food to them at nest), which are specialized on small prey, the benefits of being large are counterbalanced by greater energy requirement due to a greater number of provisioning trips. For birds of prey, this negative effect is lessened as they take proportionately larger prey and thereby make fewer trips. At three Sparrowhawk nests in England (Newton 1978), the parents made on average 8.5 deliveries per day, whereas Great Tits in a study in Japan (Royama 1966) visited their nest 150–400 times per day. Thus, from a bioenergetic point of view, nidifugous species (species where the chicks follow their parents during feeding) or species which make few provisioning trips to their young should have a greater potential for evolving sexual dimorphism either through sexual selection (Trivers 1972) favouring large males (However, Jenni (1974) showed that shorebirds (Charadriiformes) with reversed sexual dimorphism often are polyandrous, the females hence compete for males. Thus, in some cases, sexual selection can favour large females.) or through selective pressures favouring large females, or both. This prediction is supported in two ways. First, nidifugous birds are generally larger than nidicolous species and are often more dimorphic as well (Amadon 1959, Selander 1972, Wilson 1975). Second, in spite of using more energy for producing an egg than nidicolous species (Ricklefs 1974) nidifugous species often lay larger clutches (Lack 1968, Ricklefs 1974). In addition, some sea birds, e.g. Frigate birds (Fregatidae) and Boobies (Sulidae), which make few provisioning trips to their chicks (Cramp and Simmons 1977), show a slight reversed dimorphism (Amadon 1959) thus supporting the prediction.

Ricklefs (1974) stated that in passerines, the egg size – body weight relationship is nearly identical to the relationship of basal metabolic rate (BMR) and body weight. Thus, the energetic cost of egg production relative to BMR in passerine birds does not change with body size (Ricklefs 1974). In contrast, in other birds, the slope of the egg size – body weight relationship is less than that of BMR – body weight relationship (Ricklefs 1974). Hence, in non-passerine birds, egg

production is a more severe energetic strain on smaller species (Ricklefs 1974). Consequently, non-passerine females may have a selective advantage in being large, thereby reducing the relative cost of egg laying; this selection pressure is probably absent in passerines. Accordingly, the overwhelming majority of birds showing reversed size dimorphism are non-passerines (Amadon 1959) and, furthermore, except for birds of prey and the sea birds mentioned above, they are all nidifugous.

Why the link between diet and reversed size dimorphism? An apparent feature of birds of prey is that they provide relatively larger and heavier prey for their young than do other birds. Theoretical models predict that to save time and energy, the longer distances the prey should be transported the larger it should be (Schoener 1969, 1979). This is supported by field observations, showing that parent birds tend to transport the largest prey items to the nest, while they consume the smaller items themselves (Royama 1966, Root 1967, Taylor 1979). For flying animals, load and air resistance must be important factors limiting the maximum size of the prey that can be transported. An increase in body and wing size reduces the proportionate load induced by the prey. This has been demonstrated in Vespertilionid bats (Myers 1978). In these bats, where females are larger than males, Myers (1978) showed that female body size and wing size are influenced by the need to fly with large fetuses and young. However, large birds of prey, with usually high wing load (Brown and Amadon 1968), are less maneuverable, therefore, small sized prey may escape a raptor by executing sharp turns that the latter cannot match (Howland 1974). This disadvantage is probably greater for raptors which pursue agile and fast-moving prey than for the sit-and-wait predators (supported by theoretical models by Schoener 1969). In agreement with this, in highly dimorphic species of birds of prey, the smaller males, with usually low wing load (Brown and Amadon 1968), take smaller prey than do the larger females (Storer 1966, Schipper 1973, Newton 1978). Also, as a consequence of the considerations above, small raptors are better adapted to catch smaller prey: these are generally more numerous than larger prey species. This argument has been put forward by, among others, Storer (1966) and Reynolds (1972), in explaining the small size of the male as he does the main provisioning in the beginning of the nestling period.

Provisioning of nestlings by birds of prey, hence involves two conflicting selective forces, that are exceptional among birds. A large bird of prey can: (1) kill and transport large prey, (2) forage farther away from the nest, and as large prey means fewer transports, (3) spend more time on the nest, guarding and dividing food for the young (indicated by Newton (1978) to be important for getting even growth rates and reduce aggression among the young) provided the search time between each item is short enough. However, these benefits are counteracted by the lower densities of larger

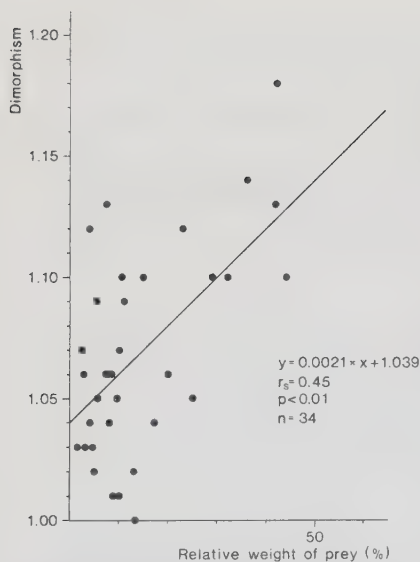


Fig. 1. Relationship between relative weight of prey and wing length dimorphism in birds of prey. Mean weight of prey and weight of the raptor (species mean) were estimated from data in Cramp and Simmons (1980).

prey. A small bird of prey on the other hand has: (1) access to a greater number of prey, and (2) requires less energy for maintenance and e.g. hunting activity.

The selective forces acting on birds of prey give the following predictions, of which none is mutually exclusive:

(1) *Species that take large prey in relation to their own body size should be more dimorphic than those that take small prey.* With respect to prey transport, reduced wing load is of no importance to raptors specialized on small prey. The greater the weight of the prey the greater the importance of reducing proportionate wing load. In addition, the smaller the relative size of the prey the greater the number of provisioning trips and, therefore, the greater the cost of being large.

Those species of Falconiformes and Strigiformes that feed mainly on invertebrates show little dimorphism in contrast to those that feed on generally larger vertebrates (Storer 1966, Brown and Amadon 1968, Earhart and Johnson 1970, Reynolds 1972, Newton 1979) (Fig. 1).

(2) *In strongly dimorphic species, the male should do most of the hunting as long as the food demands of the young remain small. The female should start hunting as*

the food demands of the young increase or as the abundance of large size prey increases.

This is valid for several Accipiters (Brown and Amadon 1968, Newton 1978, 1979). These studies also indicate that the female often does all, or most of, the incubation and brooding, and at the end of the nestling period she brings most of the food to the young.

(3) *Species that transport their prey by the crop should be less dimorphic.*

In this case crop size rather than wing load is the factor limiting the amount of food that can be transported.

The Vultures and the Secretary bird are almost monomorphic (Brown and Amadon 1968), whereas the Bat Hawk (*Macheerhampus*) is only slightly dimorphic (Newton 1979), thus supporting the prediction. But as neither the Vultures nor the Secretary Bird hunt on the wings (Brown and Amadon 1968), there is no benefit for males to be small with respect to increased hunting efficiency; thus also explaining the monomorphism in these species. The Snake eagles (*Circaetus*), which also regurgitate food for their young (Newton 1979), have a very extensible crop and can swallow larger prey (Newton 1979). They are dimorphic but still less so than Accipiters in general ($p = 0.06$, t-test, one-tailed). (The Snake Eagles /3 species/ have a mean dimorphism of 1.03, whereas other Accipiters /22 species/ have a mean dimorphism of 1.07. The measurements are based on wing length figures from Brown and Amadon (1968), and Cramp and Simmons (1980).)

There are certainly other factors outside the breeding season that regulate the body size, such as interspecific competition and migratory habits. Downhower (1976) suggested that if the resources used for egg production are accumulated immediately before reproduction, then relatively small females will be at an advantage because they can accumulate the necessary resources more quickly. Conversely, if resources for reproduction are derived from resources stored in the body before migration, then larger females will be at an advantage because they will have more reserves left for egg production. As Downhower (1976) pointed out, this might explain why migratory species of Accipiters are more dimorphic than non-migratory species (Storer 1966).

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POPULATION ECOLOGY OF THE LONG-EARED OWL

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ABSTRACT

Population dynamics and breeding biology for the long-eared owl was analysed in relation to changes in its main prey species, the field vole. The number of breeding pairs varied between 22 and one during the ten year period. Average clutch size was 4.6 eggs and average nesting success was estimated at 80 %. The average number of young leaving successful nests was 2.85. Their average weight when leaving was 219 g. Young mortality was estimated at 35 % during the nesting stage. Most of this mortality occurred during the first week after hatching. After leaving the nests, and when still dependent on the adults, about 20 % of the young disappeared, probably due to starvation and predation.

The large increase in the number of owls observed in local populations cannot be accounted for by their own recruitment. This implies a nomadic life strategy, which has probably evolved together with the asynchronously cycling small rodent populations within the distributional range of the long-eared owl in Europe. However, in my study area, with noncyclic field vole populations, there seems to be some site tenacity between breeding seasons, at least in years when voles are relatively abundant. The nomadic life strategy is briefly discussed in comparison with other owl species.

INTRODUCTION

The long-eared owl (Asio otus) is one of the most common owl species in Europe (Glutz & Bauer 1980) and its population ecology has been studied in areas with cyclic small rodent populations (mainly Microtus-species; Wendland 1957, Hagen 1965, Linkola & Myllymäki 1969, Smeenk 1972, Ziesemer 1973, Joschko 1978, Rockenbach 1978). Besides these studies, and notes in the literature, extensive data on the breeding biology of long-eared owls is available from Britain (Glue 1977).

Many owl species are known to be nomadic e.g. the short-eared (Asio flammeus) and long-eared owl, changing in density largely in accordance with vole cycles (e.g. Linkola & Myllymäki 1969), others have irruptions e.g. pygmy owl (Glaucidium passerinum; e.g. Källander 1975), whereas still others are sedentary and have small changes in density between years e.g. tawny owl (Strix aluco; Southern 1970).

This paper reports on the breeding biology and population dynamics of the long-eared owl in a South Swedish area. The data is examined in relation to changes in the density of the field vole (Microtus agrestis), the main prey species of the long-eared owl in the area (Nilsson 1981). In addition, comparisons are made with other areas and with other owl species. Their different life strategies are also briefly discussed.

STUDY AREA

The study was carried out in the Revinge area, 20 km east of Lund, in southern Sweden. The study area, of about 4300 ha, was used for farming until 1964. Since then it has been used for military training and cattle grazing. The area is an open landscape with wet meadows on peat soil (about 20 %) and open fields on mineral soil (about 60 %) with scattered deciduous woods and coniferous plantations (totally about 20 %; Fig. 1).

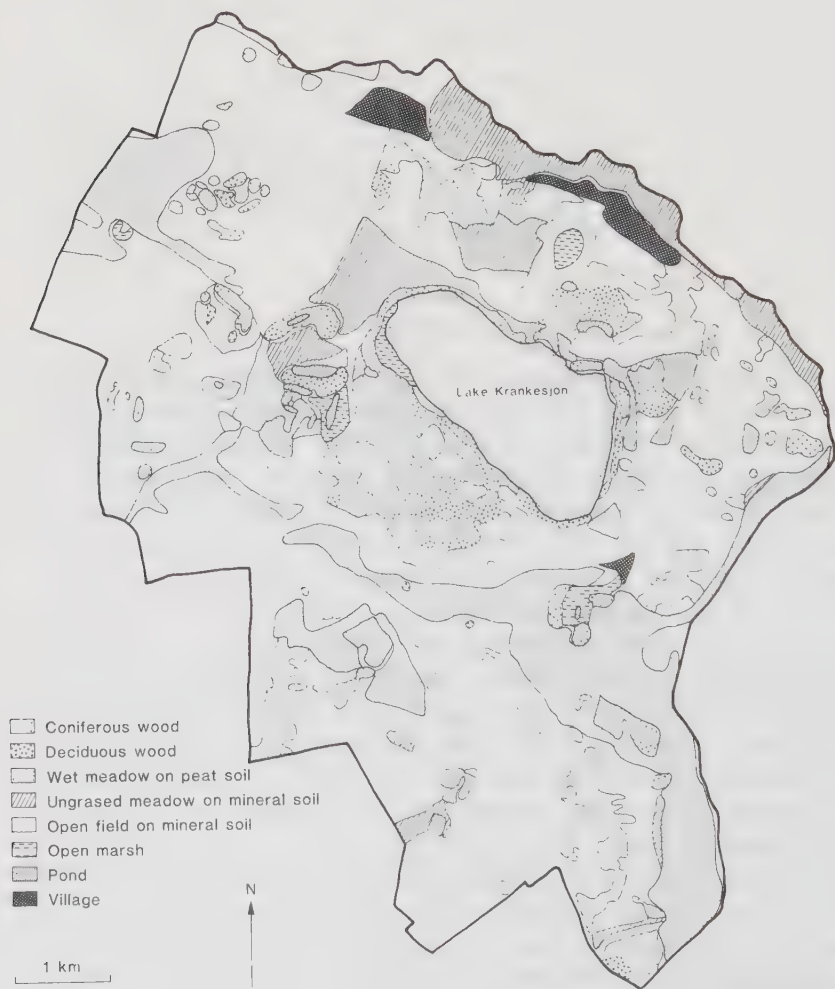


Fig. 1. The Revinge area and its main habitats.

MATERIAL AND METHODS

The long-eared owl population in the Revinge area was studied from April 1973 to June 1981. Number of broods and reproductive output was recorded throughout that period. Besides that, emphasis was put on different aspects of the owl's ecology during different years: number of pairs, breeding time, clutch size, and nestling growth was examined mainly during 1973 - 75, food choice and occurrence of non-breeding owls mainly during 1974 - 76, and winter populations mainly during 1973 - 77.

Recordings during the breeding season

During breeding time the area was systematically searched for nests during the first years (see above). Trees with suitable old twig nests were rapped and/or inspected by means of binoculars. The aim was to find the owls' nesting places just before or during the hatching period. However, only about one third of the nests were found at the egg stage, and in all about half of the nests had eggs or young when first found. Owl sightings and the occurrence of fresh pellets were also recorded.

Each nest found was usually visited once a week. If the nest contained eggs when initially inspected the eggs were weighed by a spring balance to obtain an estimate of the expected hatching time. The lightest egg was usually tapped, held to the ear, to listen for an answer from the chick, indicating hatching within a few days. The young were individually marked during the whole nest period. Firstly with nail-varnish painted in different combinations on the claws (lasting for about 10 days), and secondly, from the age of about two weeks, with standard metal bird rings. At each visit the weight, wing length, and length of the 5th primary and its vane were measured (all giving indications of age), and the nutritional status of the young and occurrence of prey items in the nest was recorded. After the young had left their nests, at the approximate age of 23 days, and before they were fully capable of flying, it was still possible to catch and measure some of them. The broods were regularly visited during the night for about two months after the young had left their nests, i.e. for as long as they were regularly begging for food, in order to establish the number of independent fledglings. In addition, from late May to late July, the rest of the area was systematically searched for food begging broods.

When estimating start of breeding and age of the young, the

fact that the eggs were supposed to be laid and hatched on alternate days and incubation to last for 28 days was used (Glutz & Bauer 1980).

Recording winter flocks

During the first years (see above) all possible roosting places were searched for owls and pellets, usually once a month. When an occupied roost was found, the owls, which usually sat very close to each other, were flushed and counted.

Prey populations

The field vole is the most common small mammal species in the area and the predominant prey of the long-eared owl for most of the year (Nilsson 1981). The seasonal changes of field vole density in the ungrazed open fields on peat soil of South Sweden is relatively high, with the lowest density in May-June (about 10 voles/ha) and the highest in September-October (about 50 voles/ha), whilst the changes between the years are relatively small (e.g. Hansson 1968, 1971, 1979, 1980).

Field vole densities were estimated by L. Hansson by two methods: Small Quadrat index trapping (Myllimäki et al. 1971) and trapping according to the Standard Minimum Method (Grodziński et al. 1966). Small Quadrat trapping was performed on abandoned fields in South Sweden, including the Revinge area, in the first two weeks of June 1972 - 75 (Hansson 1979), and in September in the Revinge area during 1971 - 79 (Hansson unpubl.). Trapping according to the Standard Minimum Method was done in the wet meadows (two large trapping quadrats in different fields) in the first two weeks of June during 1974 - 81 (Hansson unpubl., Erlinge et al. unpubl.).

The water vole population was estimated in autumn 1975, by means of snap trapping (larger snap traps), in three different habitats (B. Jeppsson & F. Schlyter unpubl.; see Erlinge 1981 for details). Detailed studies of local water vole populations have been in progress since 1979 (B. Jeppsson unpubl.).

RESULTS

Nest distribution, nesting success, and breeding density

The breeding population of long-eared owls showed large changes during the ten year period (Fig. 2, Table 1). Also, the proportion

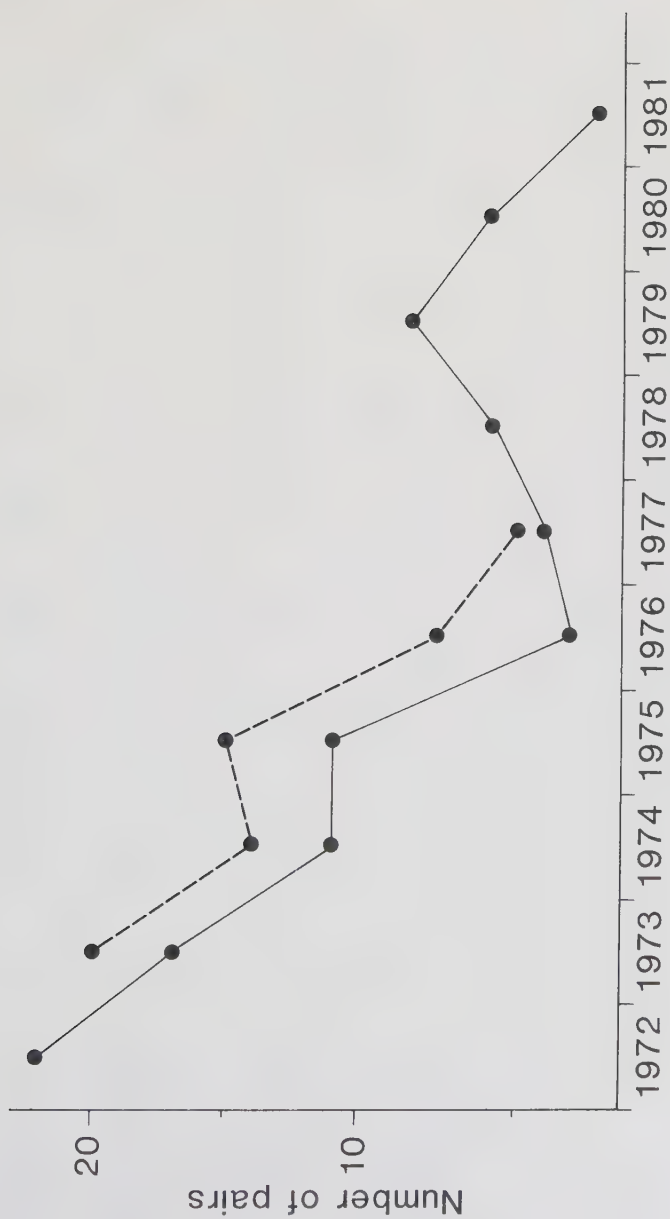


Fig. 2. The number of successful pairs (solid line), and number of pairs and sites occupied in April (broken line) in the Revinge area.

TABLE 1

Population data for the long-eared owl in the Revinge area 1972 - 81. The data from 1972 was obtained from G. Göransson, G. Högstedt, J. Karlsson, H. Källander and M. Sylvén (unpubl.).

Year	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
Number of nests found	-	20	13	13	2	3	5	8	5	1
Number of additional places occupied during at least April	-	0	1	2	5	1	-	-	-	-
Number of food begging broods	22	17	11	11	2	3	5	8	5	1
Mean number of young leaving the nests/ successful pair	-	1.82	3.00	2.91	2.50	3.00	2.20	2.13	2.20	3.00
Total number of young estimated to leave the nests (range of estimate)	-	31 (30-33)	33 (32-36)	32 (30-34)	5 -	9 (9-10)	11 (11-13)	17 (17-20)	11 (11-15)	3 -
Number of owls found dead during the year (during March - May only)	-	1(1)	1(1)	6(2)	5(4)	1(1)	-	-	-	-

of the sites which were occupied during at least the first half of the breeding season (April, but without any evidence of breeding later on in the season, varied (Table 1). Whether these sites were occupied by single owls or pairs could not be determined.

The nests were searched for during the final stage of incubation in order to reduce my own impact on the breeding success. The owls probably had the lowest tendency of abandoning their nests from that time and onwards. They showed no nest defence when the eggs were fresh, but gave warning calls and stayed near the nest, during nest inspection, when hatching time was close and from then on. At the next inspection a few nests checked with fresh eggs were found predated, probably by hooded crows (Corvus cornix). The proportion of clutches that successfully raised young was estimated in three different ways. 1. The number of recorded complete clutches that produced fledged young; out of 16 clutches, 14 produced at least one fledged young (87.5 %). 2. The proportion of all nests found at the nesting stage that produced fledged young; out of 39 nests found, 31 fledged young (79.5 %). Both these figures must be considered as maximum values of nesting success. 3. The proportion of occupied sites during 1973 - 77 that produced any fledged young (Table 1), which is a minimum value. Then, for the five year period, 44 sites out of 60 produced young (73.3 %), and 39 out of 49 (79.6 %) during the three first years when the most reliable estimates for non-breeding owls were used. However, nesting success seemed to vary between different years as indicated in Table 1, so the values must be considered as averages only (see also Newton 1979).

Breeding density varied from 0.023 to 0.51 food begging broods /100 ha, with an average of 0.20 during 1972 - 81. Correcting for an assumed average nesting success of 80 %, the maximum density increases to 0.64 pairs/100 ha, and the average to 0.25 pairs/100 ha. The density, in parts of the study area, could sometimes increase to about 1 pair/100 ha as the nests were not evenly distributed and parts of the study area seemed not to be utilized by the long-eared owls during some years (Fig. 3).

Breeding time and clutch size

The median date for the start of egg-laying during 1973 - 81 was the 15th of April, but there were considerable differences between the years. Thus, during 1973 - 75 the median dates were the 4th, 16th, and 20th April, respectively. The mean dates for the start

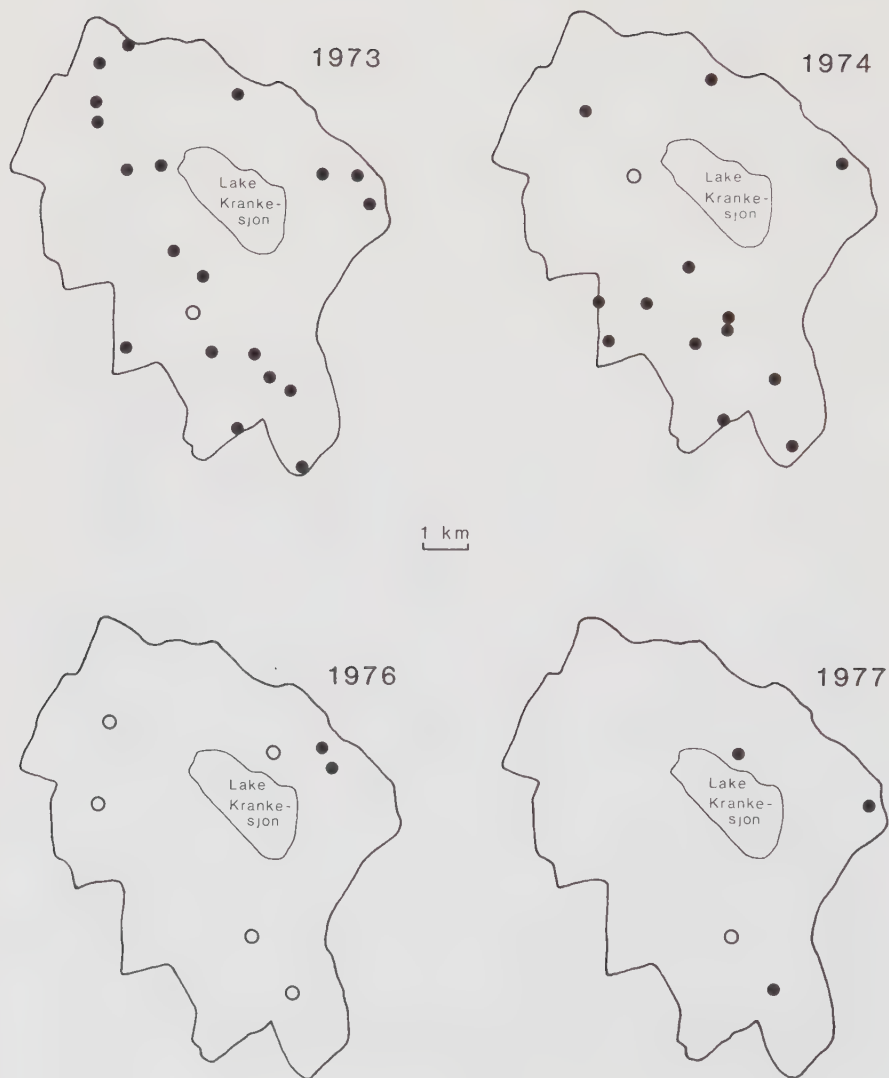


Fig. 3. The distribution of found nests (dots) and sites occupied in April (circles) during some of the years.

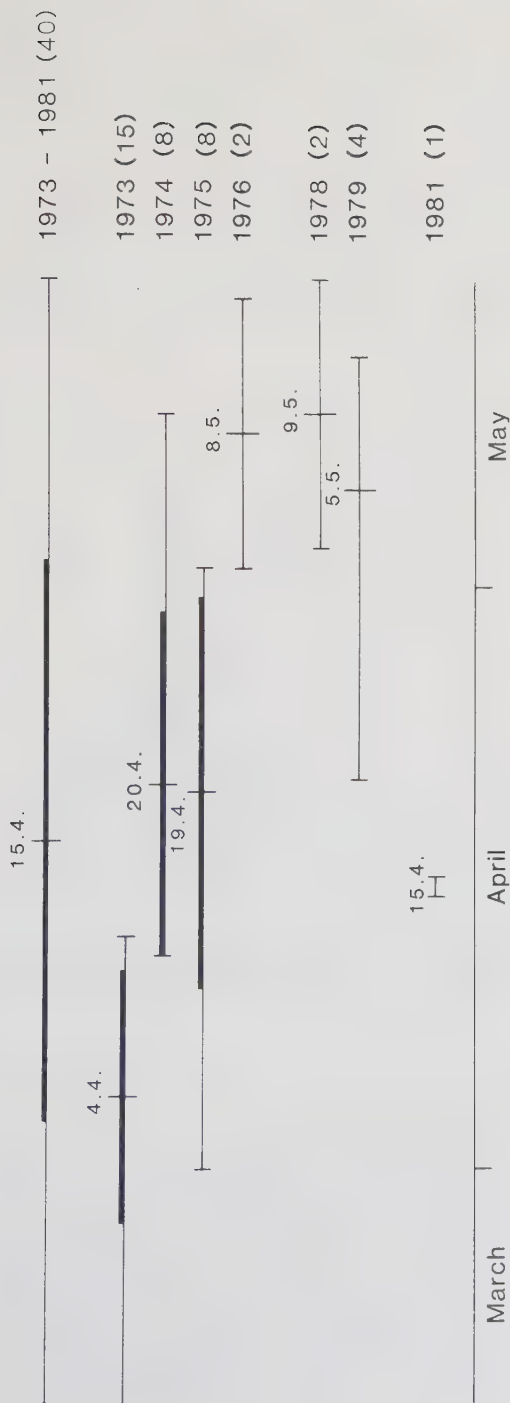


Fig. 4. The start of egg-laying for long-eared owls in the Revine area. The thin line denotes the total range for the start of egg-laying in recorded nests, the thick line its standard deviation (SD), and the central vertical line shows the mean date (also given in figures). The total number of recorded nests is given in parenthesis.

of clutches, for all years with data are shown in Fig. 4. During 1974 and 1975 egg-laying in most of the nests started later than in 1973. The few nests recorded in 1976 - 79 indicate a still later start of egg-laying.

The mean clutch sizes during 1973 - 75 were 4.3 ($n = 6$), 5.0 ($n = 5$), and 4.8 ($n = 4$) eggs, respectively. The average for all recorded complete clutches was 4.56 eggs (Fig. 5). Only three eggs, in different clutches, out of 73 (4.1 %) did not hatch. In another clutch of 5 eggs, 4 did not hatch, but this clutch was excluded as the failure was due to human disturbance.

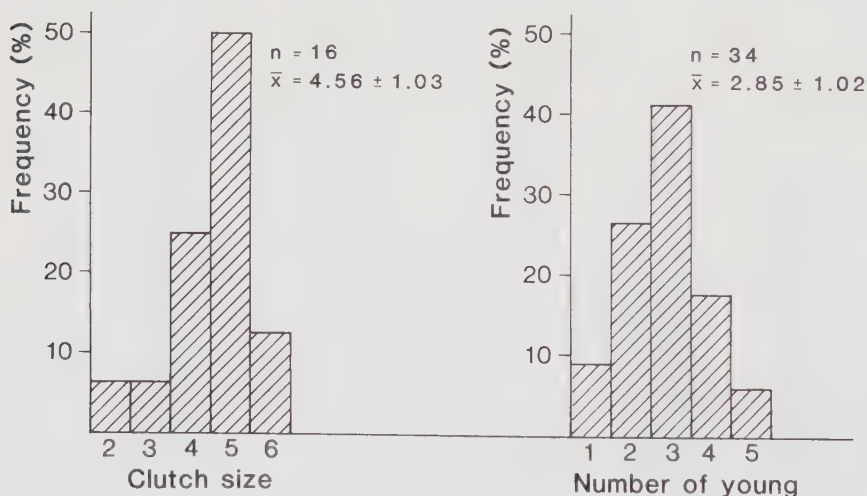


Fig. 5. The frequency distribution of clutch sizes and brood sizes (number of young leaving the nest). The distributions are significantly different (χ^2 -test, $p < 0.001$).

Nestling growth and survival

The weight of the nestlings, when newly hatched, was about 18 g. The lowest weight recorded, for a nestling surviving for at least a week, was 16.5 g. Average growth rate was higher during the first 12 days than later on (Table 2, Fig. 6). When leaving the nests the young weighed about 219 g (Table 3), without any significant differences between the years 1973 - 75 (t -test, $p > 0.10$). This is about 75 % and 90 % of the adult weights for females and males, respectively (Glutz & Bauer 1980, own observations).

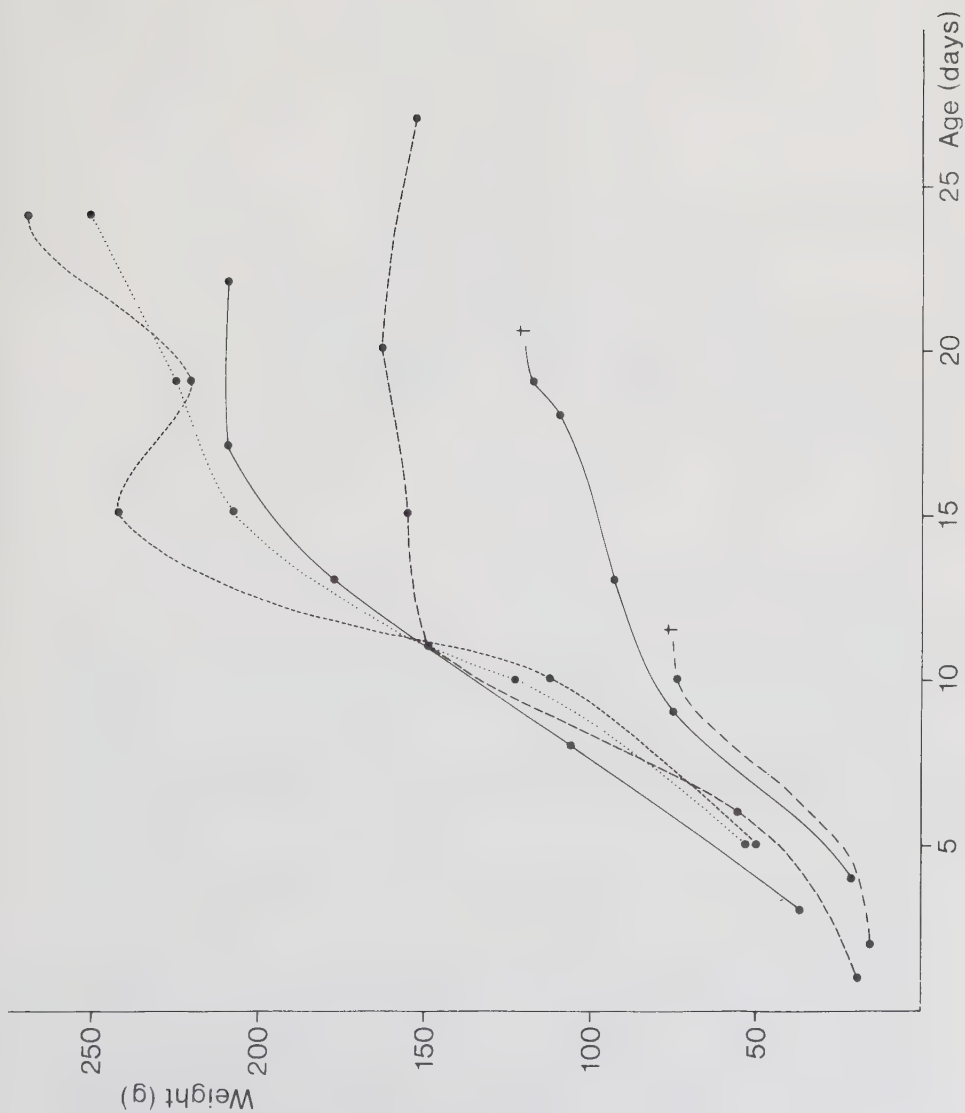


Fig. 6. The individual weight growth curves for some of the long-eared owl nestlings.

TABLE 2

Growth rate of surviving long-eared owl nestlings during two age periods; all assumed to weigh 18 g at hatching. The growth rates were statistically different ($t_{67} = 3.12$, $p < 0.005$).

Nestling age period	Mean growth rate (g/day $\pm$ SD)	n
First 12 days	10.3 $\pm$ 2.6	37
From 13th day to about 23rd day	7.9 $\pm$ 3.6	32

TABLE 3

Average weight of nestlings at the stage of leaving the nest (about 23 $\pm$ 2 days old) during different years.

Year	Mean weight (g) $\pm$ SD	Number of nestlings
1973	217 $\pm$ 31	32
1974	228 $\pm$ 26	18
1975	213 $\pm$ 28	16
All observations	219 $\pm$ 29	72

The weight distribution of the young, when leaving the nests, showed no tendency of size dimorphism, other than the great weight range (Fig. 7).

The number of young leaving the nests was definitely known in 34 broods and averaged 2.85 young/successful nest (Fig. 5). The number of young/nest varied between one and five but there were no significant differences between the years 1973 - 75 (t -test, $p > 0.20$). The estimated number of young/successful nest was in the range from 1.8 to 3.0 (Table 1).

Most of the nestling mortality occurred during the first days after hatching. Usually, one or two of the smallest nestlings disappeared, probably eaten by their larger siblings, as was observed in a few cases. The reason was obviously the insufficient provisioning of food by the male.

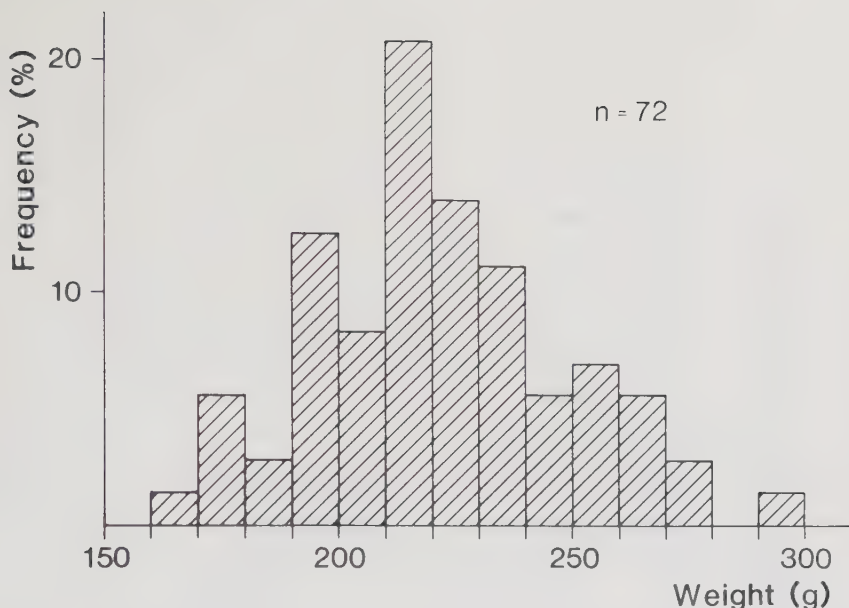


Fig. 7. The weight frequency distribution for long-eared owl nestlings when leaving their nests.

The young begged loudly for food for about two months after leaving the nest. During most of the period they are totally dependent on the adults for food, but at the end of the period they seem to hunt, at least partially, by themselves. In 29 nests the number of young leaving the nest and reaching independence could be determined. Out of 83 young, 65 survived until independence, i.e. a loss of 22 %. In one of the nests all five young were taken immediately after leaving their nest by common buzzards (Buteo buteo) who lived in an adjacent nest (about 30 m away). If these young are excluded the loss rate decreases to 17 %.

Winter populations

The long-eared owls used, most often, three communal roosting places from about September to about February (Fig. 8). The ones used varied between the winters and sometimes within one winter season (Fig. 9). However, one of them was used most frequently. At this roost the maximum number of owls, at any winter census, was estimated at about 20 owls (Fig. 9). In addition, some other places were temporarily used by the owls for roosting (Fig. 8).



Fig. 8. The position of main roosts (large stars) and some of the temporary roosts (small stars) for long-eared owls during the winters 1973 - 79. The dotted areas show the distribution of wet meadows and ungrazed open fields.

All roosting sites were in pine plantations (height about 5 m) adjacent to wet meadows. These areas contain the highest densities of field voles during autumn and winter (e.g. Hansson 1977).

The first three winters and especially 1973/74 and 1974/75 were mild, and when there was snow cover its depth was only a few cm (Fig. 9). The winters after that, and especially 1976/77, were much colder and the snow cover deeper. A hard snow storm in the last days of 1976, gave a snow cover of some dm, and appeared to have forced many of the wintering owls out of the area. Also the snow period of October - November 1975 seemed to reduce the number of roosting owls in the area. During December 1977, when initially no owls were known to roost in the area, a temporary influx of owls occurred simultaneously with a snow period.

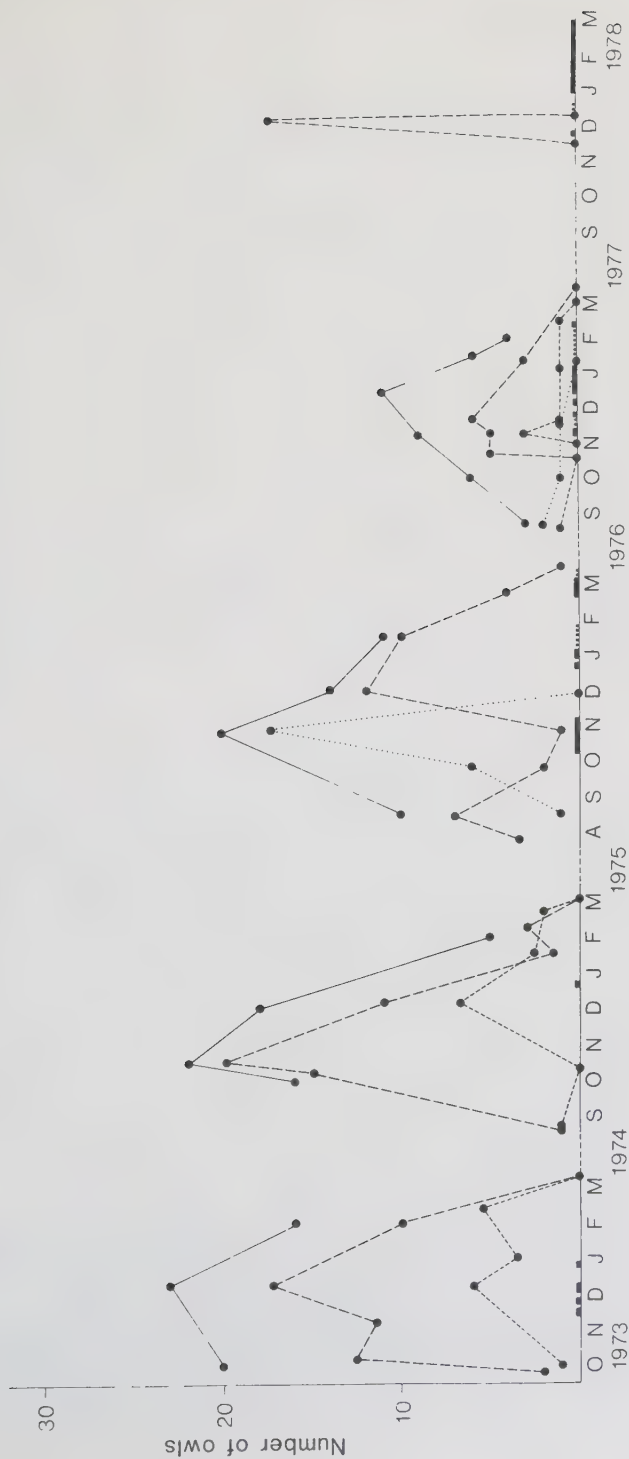


Fig. 9. The estimated number of long-eared owls in the Revinge area during the winters 1973 - 77 (solid line), and at the three main roosts (other lines; Fig. 8). The periods with complete snow cover (thick line) and scattered snow cover (dotted line) are shown on the abscissa.

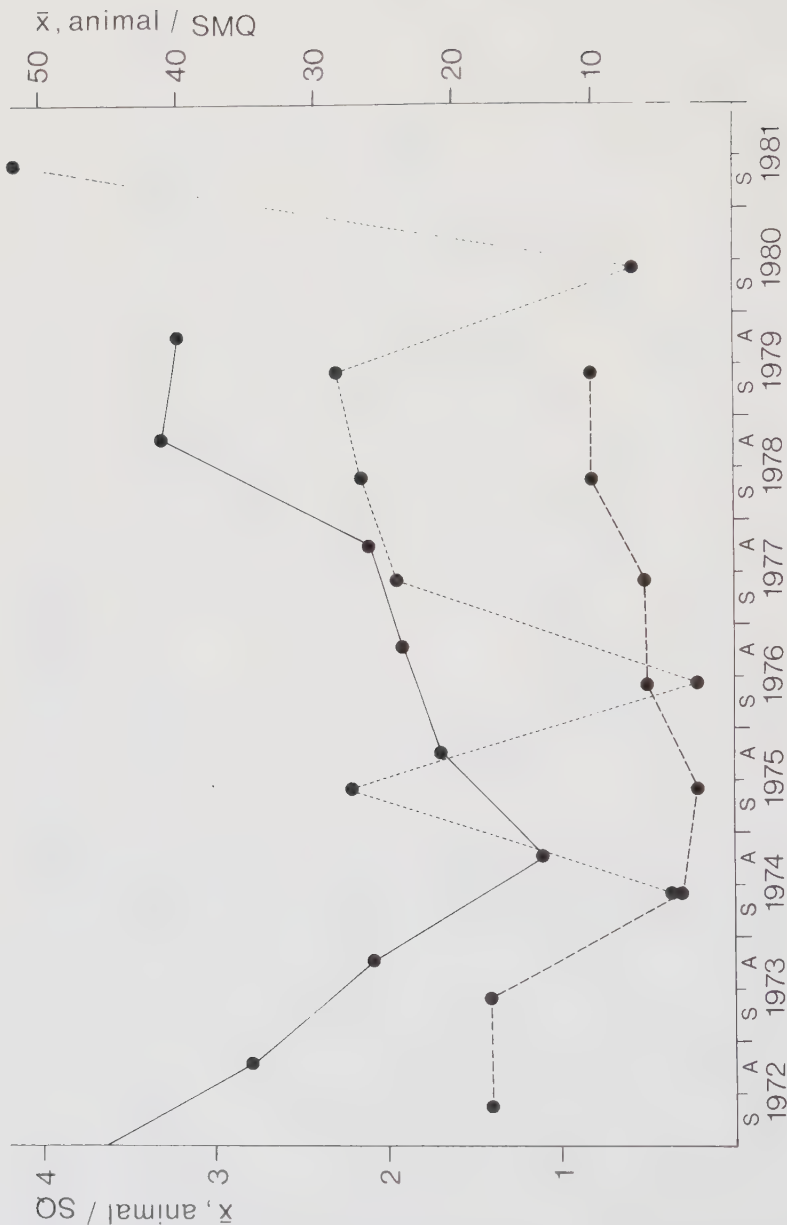


Fig. 10. The average number of field voles trapped according to the Standard Minimum Method (SMQ, Grodziński et al. 1966) in June 1974 - 81 (thin broken line), and according to Small Quadrat index trapping (SQ, Myllimäki et al. 1971) during autumn (solid line) and spring (thick broken line) 1972 - 79. The latter spring index was calculated from data given by L. Hansson (1979 and unpubl.) on number of voles trapped in southern Sweden during spring and autumn 1972 - 75 (SQ-trapping), and the number of voles trapped in autumn in the Revinge area 1972 - 79.

Prey populations

The results of the field vole trappings are shown in Fig. 10. The SQ values were always lower in the spring than the subsequent autumn. In addition, the start of field vole reproduction, as indicated especially by the proportion of juveniles in the June catches (Standard Minimum Method), occurred relatively early in 1975, 1977, 1979, and 1981. Thus, there were small variations in the spring numbers during the years. Spring abundance was particularly low 1974, compared with 1972 and 1973 (Hansson 1980), but also 1976 and 1980 had relatively low spring densities (Fig. 10).

Among the water voles there were considerable local variations in density, but, judging from the food analysis of predators, in an integrated predator - prey study in the area (Erlinge et al. unpubl.), the total water vole population did not show any pronounced between-year variations. This data together with the trapping data from autumn 1975 (B. Jeppsson & F. Schlyter unpubl.) indicated an average decrease in water vole numbers during the non-breeding season from about 8 water voles/ha in October-November to about 3 voles/ha in the beginning of May (Erlinge 1981).

DISCUSSION

Vole populations in the study area

Seasonal and between year variations in the density of the field vole population in the area is known in broad outlines (Fig. 10). The study area is heterogenous with the best field vole habitats (meadows on peat soil) scattered over the area. Thus, the distribution of the field vole population is uneven, and furthermore clumped within the patches, and this greatly influenced the catch in the trapping grids (e.g. Hansson 1971, 1980, pers. comm.). However, no statistically significant density variations were found neither between years nor between sampling areas during 1974 - 77, except for a higher proportion of juveniles due to an earlier start of reproduction in 1975 and 1977 (Hansson 1980 and unpubl.). Too little information is available on the population dynamics of the water vole, another important prey for the long-eared owls in the area (Nilsson 1981).

Breeding population density of the long-eared owl

The number of long-eared owls in an area is said to depend much on the vole density (Glutz & Bauer 1980). Thus, in areas with

cyclic small rodents, the density of owls greatly changes between years and could locally be as high as 8.2 pairs/100 ha (Joschko 1978). Usually, however, the overall density is much lower, i.e. 0.1 - 0.2 pairs/100 ha during the good years, and about 0.03 pairs/100 ha during the low years (Wendland 1957, Ziesemer 1973). These density variations are similar to those during the second half of my study. Considering the whole study period, however, breeding density variations were twice as large. Also, the number of pairs of kestrel (Falco tinnunculus) in the area, a species with almost identical diet during spring, changed in parallel with that of the long-eared owl (G. Högstedt pers. comm.). The great variation in owl numbers is surprising as the differences in spring densities of field voles between the years were small (Hansson 1980). It might be that the vole density varied around such a critical level, that even small variations in density could strongly affect the number of owls that choose to stay and breed in the area. However, the methods of estimating small rodent numbers are affected with uncertainties, and the relation between the breeding density of the owl and the field vole population is complex. Thus, there was only a tendency for the number of broods to increase with the estimated vole index in spring during 1972 - 79 (Fig. 10, SQ; $r = 0.66$, $p < 0.10$), whereas no such correlation was found during 1974 - 81 with the Standard Minimum indices (Fig. 10, SMQ; $r = 0.25$, $p > 0.10$). The number of young/successful nest was negatively correlated with the estimated vole index in spring 1973 - 79 (Fig. 10, SQ; $r = -0.91$, $p < 0.01$). This is surprising but could indicate a negative effect of intraspecific competition, on the reproductive output. However, the number of young/successful nest showed only a tendency to be negatively correlated with the number of broods ($p > 0.10$).

Time of breeding and clutch size

The start of egg-laying (Fig. 4) seems to be influenced by abundance and start of reproduction of the voles in the area (Fig. 10). In 1974, with the late start of reproduction and the low spring abundance of the field vole, a tendency for fewer early and more late clutches was found, than in 1975, when the voles started to reproduce earlier (Fig. 4). Nord (1978) found an earlier breeding start in the long-eared owl when voles were abundant; this was also indicated by Ziesemer (1973), and found for other owl species in e.g. Finland and Sweden (Linkola & Myllymäki 1969, Lundberg 1979a).

Average clutch size in Northern Europe varied between 4.0 and 5.5 (Table 4), with some of the highest values in areas with pronounced vole cycles.

Clutch size is known to decrease through the season (Lack 1954, 1966, Klomp 1970, Newton 1979). This trend was observed in 1973, although the number of recorded clutches was few ($n = 6$, $r = -0.88$, $p < 0.02$). The number of young leaving the nests showed no such trend, supporting the findings by Southern (1970) for the tawny owl. However, this is perhaps not to be expected as food abundance should be the more important factor in determining the reproductive output and perhaps also clutch size. Thus, the Ural owl (*Strix uralensis*) had larger clutches and started to reproduce earlier when food was abundant, than when food was scarce (Lundberg 1979a). This was also shown experimentally for the kestrel in The Netherlands (Drent & Daan 1980). Clutch size for many other birds of prey increases during vole plagues (e.g. Lack 1954, Newton 1979), especially so for the nomadic species short-eared (*Asio flammeus*) and snowy (*Nyctea scandiaca*) owls, where clutches of 10 or more are known during rodent outbreaks (Clark 1975, Haftorn 1971, Glutz & Bauer 1980). The long-eared owl is also said to produce up to 10 eggs (Glutz & Bauer 1980), but clutches of 6 or 7 are more frequent when food is abundant (Linkola & Myllymäki 1969). A high proportion (88 %, $n = 89$) of large clutches (> 5 eggs) was observed in Finland when voles were abundant, and an average of 44 % ($n = 16$) during all years (Linkola & Myllymäki 1969). A similar frequency was observed in Germany (48 %, $n = 29$, mostly obtained during vole peak years; Rockenbach 1978). In another part of Germany, with a high average density of owls (see above), this proportion was much lower (about 20 %, $n = 20$; Joschko 1978). Even smaller proportions of large clutches occurred in Britain (5 %, $n = 87$; Glue 1977), as well as in this study (13 %, Fig. 5).

Nestling growth and reproductive output

The growth pattern (Fig. 6) followed that which generally occurs for nidicolous birds (Ricklefs 1968). Mean weight of young leaving the nest (nests where at least two out of three young had been weighed) and the number of young leaving the nests tended to be positively correlated, however, this was not statistically significant ($p > 0.10$). The mean weight of young in the nests with three to five young leaving tended to be higher, than in nests

TABLE 4

Average clutch and brood sizes for the long-eared owl in different areas in Europe.
The number of observations is given in parenthesis.

Area	Clutch size	Number of young/ successful nest	Percentage of average clutch size not pro- ducing young in successful nests	References
Norway	-	2.77 (22)	-	Hagen 1965
Finland	4.9 (16)	3.2 (49)	34.7	Linkola & Myllimäki 1969
Great Britain	4.02 (87)	2.39 (89)	40.5	Glue 1977
N. Germany	4.2 (31)	3.2 (31)	23.8	Ziesemer 1973
N. Germany	4.70 (20)	3.2 (20)	31.9	Joschko 1978
E. Germany	-	2.40 (15)	-	Wendland 1957, 1958
S. Germany	5.48 (29)	4.04 (46)	26.3	Rockenbauch 1978
Belgium	4.51 (39)	3.69 (23)	18.2	Paulussen 1955
S. Sweden	-	2.42 (57)	-	Gustavsson 1978
S. Sweden	4.56 (16)	2.85 (34)	37.5	This study
Average	4.45 (238)	2.82 (386)	36.6	

with one or two young leaving (Median test, one-tailed, $p \approx 0.06$). These results might be due to differences in individual pairs' hunting areas (e.g. Högstedt 1980), or perhaps in the parents' ability to rear young.

A significant influence of increased food supply on e.g. breeding success and nestling growth rate and weight was found e.g. for the long-tailed skua (Stercorarius longicaudus; Andersson 1976), and has also experimentally been shown for the sparrow hawk (Accipiter nisus; Newton 1979) and for the magpie (Pica pica; Högstedt 1981). However, in this study no significant correlation was found between the number of young leaving the nest and the number of voles trapped (Standard Minimum Method) in adjacent fields, but the number of observations were few ($n = 12$). In addition, the owls largely exploit other prey species populations when they have nestlings, such as water voles and birds, especially young individuals (Nilsson 1981). Thus, it seems as if the long-eared owls, in the Revinge area, produce their clutches mainly on field voles, but feed their young substantially on other prey species.

Average clutch size was correlated with average reproductive output in successful nests (Table 4, $r = 0.76$, $p < 0.05$). This also appeared in Ziesemer's (1973) data from four years ($r = 0.96$, $p < 0.05$), with the lowest value when vole abundance was low. This would be expected if food abundance is important in determining clutch size; if food is relatively abundant when the clutch is formed then food is probably relatively abundant when the brood size is adjusted, i.e. during the first week after hatching. Hagen (1965) and Ziesemer (1973) both found a higher number of young produced/nest during vole peaks. Pettersson (1977) noted a decreasing brood size during 1957 - 76 for the long-eared and tawny owl, occurring also if the peak years only were compared. He suggested that a decreasing proportion of grazed meadows and the lowering of the field vole population, could be the reason (cf. below). On average, about one third of the eggs did not produce fledged young, even in the successful nests (Table 4), probably due to starvation. This proportion is expected to be lower in cyclic areas, due to richer food supply during peak years and nomadism, but the pattern is unclear (Table 4; see also below and Newton 1977).

The nesting success in this study was estimated at about 80 %. Rockenbach (1978) obtained a similar value (70 %), whereas Glue

(1977) found a much lower value (41 %) in Britain. However, the long-eared owl was persecuted there and one sixth of the losses were definitively caused by man (see also Newton 1979).

Indications of site tenacity and population dynamics

It has been suggested, that a pair of long-eared owls may breed in the same place during consecutive years, and that the young can breed in their native area the next year (Wendland 1957, Joschko 1978). Data obtained in this study makes a preliminary test of these ideas possible. The proportion of owls occupying the same or adjacent sites during consecutive years varied between zero and 86 % during this study. The proportion of occupied sites, was higher during the initial four years of population decrease (1973 - 76) than later on (Table 5). The total number of sites in the study area, suitable for long-eared owls is at least one hundred, so the probability of owls nesting in the same site just by chance should be small. Assuming a death rate of 31 % for the adults (Glutz & Bauer 1980) and complete site tenacity, up to 70 % of the owls could breed in the same site as the preceding year.

TABLE 5

Proportion of sites (nesting sites and other sites occupied in April) occupied by long-eared owls during consecutive years. The number of occupied sites/number of sites the preceding and following year, respectively, is given in parenthesis.

Period	Mean proportion of occupied sites within 350 m of sites occupied the preceding year (%)	Mean proportion of occupied sites within 350 m of sites occupied the following year (%)
1973 - 76	70 (38/56)	52 (38/71)
1977 - 81	20 (5/23)	17 (5/29)
1973 - 81	42 (43/79)	33 (43/100)

No significant correlations were found between the number of broods one year and the summed mean temperatures during any of the two winter periods October-March and November-February the preceding year ($p > 0.10$), although there were positive trends (cf. Källander & Karlsson 1981). The number of broods one year was positively correlated with the number of broods the next year

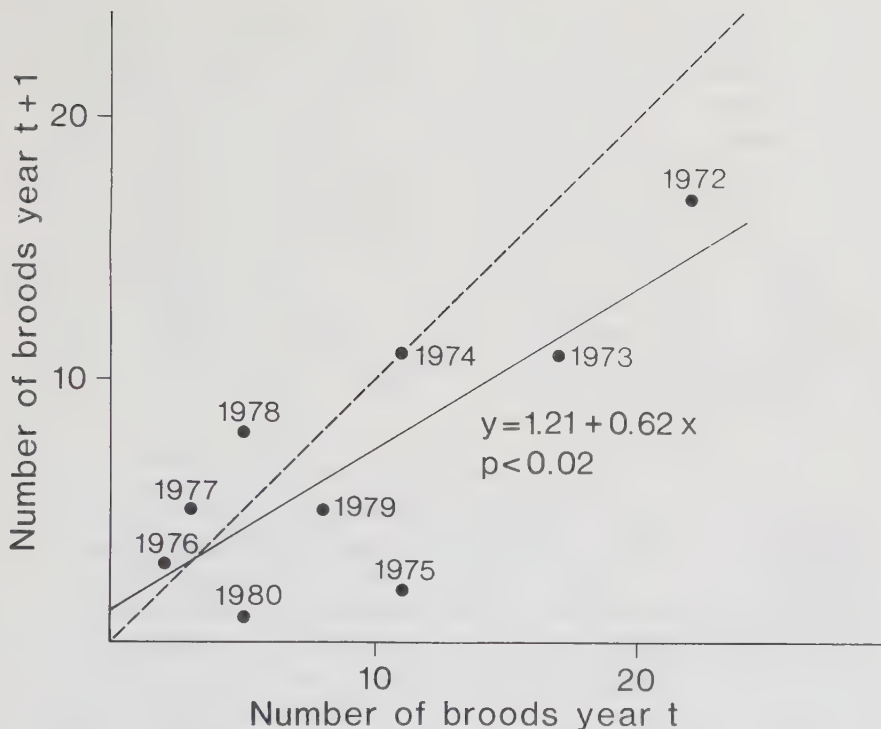


Fig. 11. The number of long-eared owl broods during one year in relation to number of broods the following year (solid line, $r = 0.80$). The broken line indicate complete dependence.

(Fig. 11). It thus seems that, at least for areas with minor changes in the vole populations, the long-eared owls, and possibly some of their offspring, try to stay and breed in the same area as long as the food situation allows this (cf. Andersson 1980). This strategy has been suggested for the great grey owl (*Strix nebulosa*; Wahlstedt 1976). In contrast, most of the long-eared owl pairs in Scotland and other parts of Britain stay in their territories during the whole year (I. Newton pers. comm., BOU 1971). The relation between breeding and wintering populations in most other areas are, however, unclear (e.g. Källander 1977, Lundberg 1979b).

The Swedish long-eared owls move southwards and, at least some of them, leave the country mainly in October-November, especially during hard winters and particularly after a year of good reproduction, many owls were ringed at Swedish bird observatories

in the autumn and in the autumn of the following year (Roos 1975, 1976, Cronert et al. 1978, Nord 1978, Hjort et al. 1981). Also in October-November the number of owls in winter flocks in the Revinge area increased (Fig. 9). If this was caused by the aggregation of local owls or by an influx of owls from distant areas is not known. The number of breeding owls and young that wintered in the area seemed, however, to be low (Table 1, Fig. 9). Two recoveries of owls ringed in the area gave the same mixed picture. An owl ringed in a winter flock in the middle of February was found freshly dead two months later, during the breeding season, 30 km south of the study area. Another one, ringed as nestling 1973, was found dead on one of the main winter roosts in January 1976 (see also Källander 1977).

Population dynamics and vole cycles

In areas with cyclic vole populations the long-eared owl has pronounced peaks coinciding with the vole peaks (e.g. Hagen 1965, Rockenbach 1968, Linkola & Myllymäki 1969). Thus, for the long-eared owl, the coefficient of variation (CV) in the number of pairs or broods varied from 82 to 130 % (Table 6, Pettersson 1977, Joschko 1978), whereas in three tawny owl populations, two of which were in the same areas as above, corresponding figures varied from 20 to 37 % (Pettersson 1977, Delmée et al. 1978, Gustavsson & Thorin 1981). In my study area these values, for the number of broods, were in the lower part of these ranges; 80 % and 18 % for the long-eared and tawny owl, respectively, consistent with the relatively small inter-year changes in field vole abundance (Hansson 1971). These sudden increases in the number of breeding long-eared owls can not be explained by reproduction for a local population. The average annual number of young that must be produced to maintain a stable local population of long-eared owls (recruitment standard) is 1.3 young/pair, assuming the mortality rates given by Glutz & Bauer (1980; see Fig. 12), breeding the first year, and equal sex ratio (method according to Henny & Wight 1969, Henny et al. 1970). If all sites, in the Revinge area, occupied during any of the breeding seasons 1973 - 77, are considered as occupied by pairs (Table 1), then the actual average reproductive output was 1.8 young/pair; which is a minimum figure. If only found nests were considered, the average value was 2.2 young/nest; a maximum figure. Then the potential increase rate of pairs could be calculated to be in the range 12 - 22 %. Further,

TABLE 6

Population dynamics of the long-eared owl in some Swedish provinces. The data was obtained from Gustavsson & Thorin (1981) from the province of Småland (about 200 km NE of the Revinge area), Nord (1978) for the province of Södermanland (about 400 km NNE), Martinsson (1975, 1977) and Carlsson (1980) for the province of Värmland (about 500 km N). Most of the broods in Värmland 1973 and 1974 occurred in different parts of the province (Martinsson 1975). Vole peaks, as stated by the authors, are indicated by stars (*). See also Table 1.

Province	Kind of measurement	1973	1974	1975	1976	1977	1978	1979	Coefficient of variation (%) ($\frac{SD}{\bar{x}} \times 100$)
Småland	Number of territorial owls and number of broods	33*	8	2	11	14*	11	6	82
Södermanland	Number of broods reported in enquiry	73*	27	2	12	72*	-	-	90
Värmland	Number of territorial owls reported in spring	7*	82(*)	3	7	24*	24	4	130
	Number of broods reported	53	122	3	14				

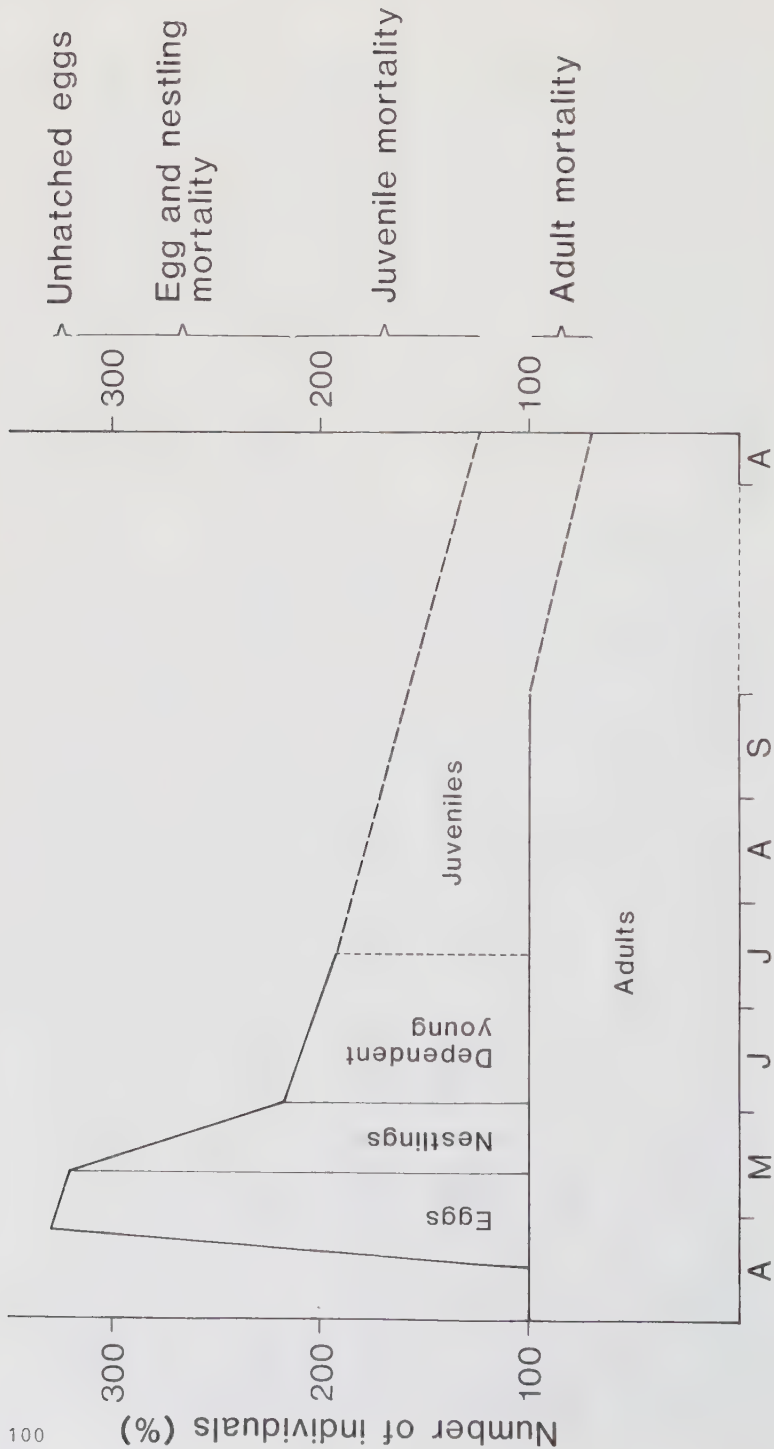


Fig. 12. The schematic representation of a breeding cycle in the long-eared owl, using results from this study and assuming an annual mortality rate of 52 % in the juveniles and 31 % in the adults (Glutz & Bauer 1980).

assuming the mortality rates given by Glutz & Bauer (1980) combined with breeding data from this study, the potential increase rate in pairs would be only 12 % for the local population (Fig. 12). Then, to make the low capacity for increase balance with the population dynamics observed, the long-eared owls should breed somewhere, almost every year (cf. Lundberg 1979b), underlining the nomadic life strategy of the species, and indicating that the vole cycles in different regions would be unsynchronized (see also Horn 1978, Andersson 1980). This is also suggested by data in the literature (Table 1 and 6, references below; see also Hansson & Larsson 1980, Hansson 1980). Thus, simultaneous peak numbers of voles and long-eared owls occurred in Norway 1958 (Hagen 1965), in the middle of Finland 1962 (Linkola & Myllymäki 1969), in south central Sweden 1957, (1958), 1961, 1973, (1974), and 1977 (Pettersson 1977, Table 6), in northern Germany 1965, 1968, 1971, and 1974 (Ziesemer 1973, Joschko 1978), and in southern Germany 1961 and 1966 (Rockenbach 1968, 1978). The population in the Revinge area showed a decreasing trend, although there was a small peak 1979. This decrease might have been caused by the continuous but slow overgrowing by bushes (mainly Salix-species) of some of the wet meadows, or by draining some of them (cf. Pettersson 1977). Another reason could be increased diffuse competition from the generalist predators in the area e.g. foxes (Vulpes vulpes), due to the low rabbit (Oryctolagus cuniculus) population 1977 - 80 (Erlinge et al. unpubl.).

In conclusion, I suggest that the long-eared owl has evolved together with the asynchronous vole cycles, and that it largely follows the population strategy suggested for the Tengmalm's owl (Myserud 1970), later, however, contradicted partly for that species by Lundberg (1979b). The same nomadic pattern is shown by some other owl species specializing on voles and lemmings e.g. short-eared and snowy owls (e.g. Pitelka et al. 1955, Haftorn 1971, Glutz & Bauer 1980), although these species seem to be still more extreme in their nomadic movements.

The evolution of life history tactics is dependent of different factors, e.g. clutch size and juvenile and adult mortality rates (see review by e.g. Sterns 1976). A model of the relative merits of nomadism and site tenacity for cyclic versus randomly fluctuating food environments (Andersson 1980) showed that nomadism was favoured because of e.g. large clutch size (b), relatively high juvenile (S_1) and low adult (S) survival, and high probability of finding a good area in a cyclic food environment.

Site tenacity was favoured because of e.g. short interval between the good years, and a low probability of finding a new good area. Based on the values presented in Table 4 of the number of young (b) and the survival rates ($S = 0.69$, $S_1 = 0.48$) given by Glutz & Bauer (1980), the relation $b \cdot \frac{1}{S}$ (Fig. 1 in Andersson 1980) actually lies in such a range (1.7 - 2.8) that either site tenacity or nomadism can be favoured in the long-eared owl, depending on the probability of finding a new good area and the average interval between successive good years. Other important factors, not accounted for in the model are the food abundance during the low years and, as pointed out by Andersson (1980), the risk of increased mortality during nomadism, especially in the juveniles. The number of small rodents in areas such as e.g. northern Sweden is usually low one or two years after a peak year, but during the other years usually similar or larger than the average for e.g. southern Sweden (e.g. Hansson 1980). Thus, at least some of the owls could possibly stay and reproduce in a cyclic area for more than a peak year. Furthermore, the observation that different small rodent species tended to have different intervals between their peak years (Wendland 1981) makes this suggestion more probable, as do observations on population dynamics of long-eared owls in some areas, e.g. Britain (see above) and Germany (Wendland 1957, Joschko 1978). However, it is advantageous for the owl parents that some of their offspring disperse even when the local environment has not deteriorated and even when the process of dispersal itself incurs considerable mortality (Hamilton & May 1977, Horn 1978). Furthermore, successfully breeding adult owls are probably more likely to stay in their familiar area than are the juveniles (e.g. Newton 1979).

Thus, more precisely, I suggest that the best strategy for an adult long-eared owl, i.e. the one giving the highest life-time fitness, should be to stay in the same or adjacent area as long as it can reproduce successfully, in order to minimize the risk of death due to long distance migration, and to exploit the familiarity with the area and thus perhaps increase its hunting efficiency. Whenever the probability of successful reproduction the next season, maybe monitored by food abundance during autumn and winter, is lowered, it should leave and try to find an other area. The latter prediction is probably also affected by the number and type of food competitors in the area. The most probable choice for the juveniles, to speculate further, is likely to be searching for a good area away from their birth place, i.e. juvenile nomadism

(Andersson 1980), supported somewhat by observations at Swedish bird observatories after peak years (see above).

In raptors a size-related r-K-continuity (MacArthur & Wilson 1967) has been suggested (Newton 1979). However, Horn (1978) suggested that the "positive feedback for both extremes of r-selection and K-selection suggests that animals in nature may show extreme characteristics more often than an intermediate set of characters". This seems to prevail among the owls, which apparently are divided into two more or less clear extremes, both, however, with small and large species. Firstly, there are the more or less nomadic food specialists, with relatively large clutches, e.g. long-eared owl and snowy owl, and secondly, the resident species with a more diverse diet, and smaller clutches, e.g. tawny owl and eagle owl (Bubo bubo). Some other species, however, seem to be intermediate e.g. with a sex-differentiated strategy as in Tengmalm's owl (Lundberg 1979b). Perhaps, also other species deviate; little information is available for e.g. the hawk owl (Surnia ulula) and pygmy owl (Glaucidium passerinum), although they are known to be irruptive (e.g. Hagen 1956, Källander 1975, Kellomäki 1977, Glutz & Bauer 1980).

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